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TO

MY WIFE

THIS WORK IS AFFECTIONATELY DEDICATED

AS A SMALL ACKNOWLEDGMENT OF THE INTEREST EVINCED AND

ENCOURAGEMENT EXTENDED IN ITS COMPLETION,

BY

THE AUTHOR.



## P R E F A C E .

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To those familiar with the many excellent German, French, and English treatises upon Physiology, it may appear strange that the author should feel it incumbent upon himself to offer one more contribution upon such a well-worn theme. The experience, however, of the past eight years, as Professor of the Institutes of Medicine or Physiology in the Jefferson Medical College of Philadelphia, has convinced the author that there is a want felt by students and practitioners of medicine for a systematic work, representing the existing state of physiology and its methods of investigation, and based upon comparative and pathological anatomy, clinical medicine, physics, and chemistry, as well as upon experimental research. It is the hope of the author that the present work, embodying essentially his teaching, will not only supply such a want, but will facilitate and stimulate the study of this most important branch, the institutes, that is to say, the foundation of all rational medicine. The author takes much pleasure in here expressing his acknowledgments to Dr. A. P. Brubaker, Demonstrator of Physiology in the Jefferson Medical College, for the assistance rendered in the performance of the experimental part of the work; to Arthur E. Brown, Esq., Superintendent of the Zoölogical Garden, of Philadelphia, for the many facilities and courtesies extended in the dissection of the rare animals that have died at the Garden, the results of which are frequently made use of in the work, and to Dr. Lawrence Wolff, Demonstrator of Chemistry in the Jefferson Medical College, for the favor of seeing the work through the press.

HENRY C. CHAPMAN.

PHILADELPHIA, October 10, 1887.





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# PHYSIOLOGY.

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## INTRODUCTION.

PHYSIOLOGY, from the Greek *φύσις* and *λογος*, literally means a discourse on Nature. At the present day, however, the word has not such an extended significance, physiology as understood by naturalists and physicians meaning the study of the functions or uses of the parts of which living beings consist.

I use the word parts, in preference to that of structures, inasmuch as there are beings like the monera, simple masses of a jelly-like substance or protoplasm, which are so structureless and unorganized that great difficulty is experienced in classifying them, it being questionable whether they should be ranged among plants or animals, or relegated to an intermediate kingdom, the "Protistenreich" of Hæckel,<sup>1</sup> or, as Huxley<sup>2</sup> expresses it, a sort of a biological "no man's land." Indeed it has been doubted whether the term living at all could be properly applied to the monera in the same sense in which that word is used in reference to the higher animals. As the totality of the functions or uses of the parts, structures, or organs of which living beings consist, constitutes their life, I may define Physiology therefore as the study of life or of function.

Necessarily from the definition, Physiology presupposes a knowledge of anatomy or structure. The relation of the two may be compared to the study of a clock when at rest and when going.

The anatomist studies the form and relation of the weights, the pendulum, the hands, etc., at rest; the physiologist, the fall of the weight, the swinging of the pendulum, the movement of the hands. Anatomy is the statical, physiology the dynamical, part of biology.

As well might the mechanic hope to understand the movements of the clock and to regulate it without a knowledge of the parts composing it, as for the physiologist to understand the motions of the living body without a previous knowledge of its structure.

Anatomy and physiology are so intimately associated that, philosophically, they should be studied together; indeed, to separate them, except for the convenience of teaching, is highly illogical.

As Hyrtl<sup>3</sup> well observes, "Anatomy, unassociated with physiology, is a mindless study and does not deserve the name of a science. Can one study the arrangement of a machine without any reference to its object?

<sup>1</sup> *Generelle Morphologie*, Bd. 2, S. xxii. Berlin, 1866.

<sup>2</sup> *Physical Basis of Life*, p. 129. *Lay Sermons*. New York, 1871.

<sup>3</sup> *Lehrbuch der Anatomie*, S. 18. Wien, 1881.



It is possible simply to view the harmoniously arranged parts of a whole, simply to stare at it without reflection. The anatomist can undertake no investigation without considering the physiological questions involved. The paths of both sciences meet and cross each other in so many places that there are but few divergent points."

In beginning the study of any subject not only is it indispensable that the object of the investigation should be clearly defined, but it is proper that relation to knowledge in general should be pointed out.

The classification of the sciences has been a vexed one from the time of Bacon<sup>1</sup> to Comte.<sup>2</sup> This, from the nature of things, might have been expected; for there are no sharply defined lines in nature; one science encroaches so upon another that it is impossible to say where the one ends and the other begins. All classification, therefore, must be imperfect. The following one, that of Comte, is open to many criticisms, as shown in the masterly essay of Spencer.<sup>3</sup>

TABLE I.

|                                   |   |              |   |          |   |             |
|-----------------------------------|---|--------------|---|----------|---|-------------|
| Classification<br>of<br>Knowledge | { | Mathematics. | { | Botany.  | { | Anatomy.    |
|                                   |   | Astronomy.   |   |          |   |             |
|                                   |   | Physics.     |   |          |   |             |
|                                   |   | Chemistry.   |   |          |   |             |
|                                   |   | Biology.     |   |          |   |             |
|                                   |   | Sociology.   |   |          |   |             |
|                                   |   |              |   | Zoölogy. |   | Physiology. |

Admitting its many faults, I make use of it here on account of its brevity simply to indicate the position of Physiology relatively to that of other kinds of knowledge.

It will be seen, from the table, that the study of plants and animals constitutes the subject-matter of Biology.

The second division of this grand science comprehends all that is known of the structure, functions, habits, geographical and geological distribution of animals; therefore, the study of animal functions or animal physiology is a subdivision of Zoölogy. In the same manner, vegetal physiology forms a part of Botany. Human physiology, a part of general animal physiology, forms the subject of this work.

If the sciences are studied in the order in which they follow each other in Table I., then the inorganic will precede the organic. This is the logical order and historically the one in which they were, generally speaking, cultivated, for the phenomena of the inorganic world are less complex and more easily generalized than those of the organic, and, therefore, more readily investigated. Wherever practicable, the historical order will be found to be the best one to pursue in the study of any science; indeed, as we proceed, it will be seen that the phenomena of physiology depend upon physical and chemical laws, and that probably, with the advance of knowledge, the whole subject will be treated as a branch of molecular physics—hence the indispensability to the student of physiology of a knowledge of physical and chemical science. Ample illustrations of the value of such knowledge will be given when

<sup>1</sup> De Augmentis Scientiarum.

<sup>3</sup> Genesis of Science. Essays. London, 1868.

<sup>2</sup> Cours de Philosophie Positive.

the special functions are considered. The special senses of sight and hearing, for example, depend for their successful study upon familiarity with optics and acoustics; the investigation of the circulation is a question of hydraulics; that of secretion, of organic chemistry.

By referring to Table I., it will be observed that Botany comes before Zoölogy; where practicable, its study should precede that of Zoölogy, for plants serve to bridge over, to a certain extent, the gap between the mineral and animal world, and at different points touch the confines of these two kingdoms. Further, with some exceptions, plants are destitute of a nervous system, and even if extended investigation should show that their nervous system is more developed than now it is supposed to be, it would exercise a small influence as compared with that of the higher animals. Plants, therefore, offer a favorable opportunity of examining the processes of nutrition uninfluenced by the nervous system.

When we come to examine the circulation, digestion, etc., in man, we shall see that these functions are greatly modified by the nervous system; hence the advantage of studying nutrition in lower organizations where these disturbing elements are eliminated.

Having endeavored to define the object of our study, and to indicate its limits and relation to knowledge in general, let me now consider the different methods by which human physiology can be investigated—and, first, a great deal can be learned of the functions of the human body by careful reflection on the structure of the same. Haller<sup>1</sup> says: “and first the fabric of the human body is to be learned, whose parts are almost infinite. Those who would study physiology separately from anatomy certainly seem to me, can be compared with mathematicians who undertake to express, by calculation, the forces and functions of a certain machine of which they have learned neither disks, wheels, measures, nor material. Truly I am persuaded that we know scarcely anything of physiology unless we have learned it through anatomy.”

Undoubtedly, the functions of many organs might be inferred from the thorough study of their structure. As a matter of history, the demonstration of the valves in the veins by Fabricius to Harvey was one of the important facts that first suggested to the latter to investigate the flow of the blood.

The functions of certain nerves will probably be never definitely settled until anatomy has determined whether they terminate in muscle, gland, or sensory organs.

Those grand old anatomists, Eustachius, Fallopius, Vesalius, with their physiological followers, Harvey, Haller, and Hunter, have well illustrated in their works the important relations of anatomy to physiology.

Not only, however, is a knowledge of general descriptive anatomy necessary, but it is indispensable also that the student who hopes to cultivate physiology with any success, must have a thorough training in histology, or the science which has for its object the study of the tissues.

The necessity of a thorough knowledge of structure, in order to

<sup>1</sup> *Elementa Physiologiæ. Lausannæ, MDCCLVII. Preface, p. 1.*



understand function, is so obvious that it seems superfluous to dwell further upon it. Pathology furnishes valuable data to the student of human physiology. Where disease is restricted to one organ, and when it is noticed that with the destruction of the tissues composing it a particular function gradually weakens and finally disappears, it is a logical inference that the loss of function is dependent upon the loss of structure. In this way the uses of many parts might be ascertained—hence, the importance of carefully kept clinical records and thorough post-mortem examination.

Suppose, for example, that, associated with loss or want of speech, in the majority of instances it is found, after death, that a particular convolution in the hemisphere of the brain is either wanting, undeveloped, or diseased—it would be a fair conclusion that the faculty of speech was connected, in some way, with this particular convolution, especially if it was clearly shown that the facts were not mere coincidence, but bore the relation of cause and effect. Or take the case of a human being suddenly paralyzed upon one side of the body both with reference to sensation and motion, and post-mortem examination revealed that certain parts of the opposite side of the brain were affected, as in apoplexy, for example. It would be natural then, to consider that the parts affected in the one side of the brain presided over the opposite side of the body and extremities—or, take the case of a man suddenly stabbed in the back-bone, the instrument penetrating only half-way through the spinal cord, and the patient loses voluntary motion on the side of the wound, and sensation on the opposite side—the view that the sensory fibres decussate in the cord, and the motor ones in the medulla would be confirmed.

While, according to many thinkers, clinical medicine and morbid anatomy alone will not furnish data sufficient to deduce a physiology and a rational pathology, undoubtedly such facts as the above are invaluable as aids in throwing light upon the still obscure functions of the nervous system and the uses of other structures in the human body.

The admirable observations of Beaumont<sup>1</sup> and Budge<sup>2</sup> upon human beings, in whom the stomach and intestine had been wounded in such a manner as to render them susceptible of experiment, are illustrations of the application of pathological cases to the study of physiology.

When the vast complexity of structure exhibited by the human organization is considered, it becomes evident that any investigation of its function, however extended, if it be confined to man alone, can lead to but very limited results.

Comparative anatomy has shown, however, that the life of the animal kingdom is a grand panorama, each fleeting form, as it passes before the view, recalling that which has just passed, foreshadowing that which is to come; the simplest of living beings, so lowly organized and transparent that their entire life processes can be observed by the microscope, leading through intermediate forms to higher types of life, closely approaching that of man himself. With the development of additional structures, we find correspondingly increased functions, and infer that the new function is due to the new structure.

<sup>1</sup> Experiments and Observations. Plattsburg, 1833.

<sup>2</sup> Virchow's Archiv, Bd. xiv. S. 140.



The comparative method of investigation is therefore the opposite of the pathological one, by which, as we have seen, the use of a structure is inferred from loss of function dependent upon the loss of structure.

In the hands of Harvey, Hunter, Cuvier, Muller, Milne, Edwards, Owen, comparative anatomy has proved of invaluable service in the study of physiology.

In his great work, Harvey<sup>1</sup> states "that if anatomists had given to the organization of the inferior animals the same attention that they devote to the structure of the human body, the question of the circulation would long since have been determined."

Observations upon the enlargement of the collateral vessels in the horns of the deer when in the velvet after ligation of the carotid, suggested to the great physiological surgeon, John Hunter,<sup>2</sup> the idea of the collateral vessels maintaining the circulation in the thigh after ligation of the main trunk.

The ligation of the carotid in the dog,<sup>3</sup> and of the femoral in the same animal, done by Home<sup>4</sup> at the suggestion of Hunter, having further convinced the latter of the feasibility of ligation as a cure for aneurism, Hunter tied the femoral artery in the celebrated case of the coachman suffering from popliteal aneurism and thereby introduced a most capital improvement in surgery.<sup>5</sup>

To study the physiology of man without the slightest knowledge of life as exhibited in the lower animals is as if one would attempt to master the steam engine without any acquaintance with the elementary laws of heat or mechanics, or to investigate a magnetic apparatus without knowing anything about the simple facts of electricity.

As the study of comparative anatomy, in its application to human physiology, at the present day, is very much neglected, it may not be superfluous to offer a few instances as illustrations of the importance of the study in this respect. For example, from the fact of the bile and pancreatic juice passing into the alimentary canal at the same point in man, it is impossible to say to which of these fluids the changes exhibited after their mixture with the food are due.

By examining the rabbit or the beaver, however, we find that the opening of the pancreatic duct into the intestine is situated twelve inches and more below that of the bile-duct. Hence, the different changes exhibited by the food as it is successively affected by these secretions, can be perfectly observed by killing a rabbit or beaver in full digestion. Indeed, as we shall see, it is in this way the emulsifying power of the pancreas is usually demonstrated.<sup>6</sup> Again, the question as to whether the bile is a secretion or an excretion finds its answer in the structure of the doris,<sup>7</sup> a little mollusk in which the liver has two ducts, one of which carries the bile into the alimentary canal, where it mixes with the food, while the other removes it at once from the body, showing that the bile, in this case at least, is both a secretion and an excretion.

<sup>1</sup> De Motu Cordis, p. 33. Frankfort, 1628.

<sup>2</sup> Works, edited by Palmer, vol. iii. p. 201.

<sup>3</sup> Ibid., vol. i. p. 444.

<sup>4</sup> Ibid., vol. iii. p. 597.

<sup>5</sup> Experimental Physiology, p. 39. Owen London, 1882.

<sup>6</sup> Bernard : Physiologie Experimentale, tome ii. p. 179. Paris, 1856.

<sup>7</sup> Cuvier : Memoires Pour Servir a l'Histoire et a l'Anatomie des Mollusques. Paris, 1817. Memoire sur le Genre Doris, p. 16.

One of the best established facts in physiology is that the intellectual faculties depend upon the development of the brain, both in reference to quantity and to quality. This is well seen when the brains in a series of animals are compared with reference to their intelligence. With the gradual addition of certain parts of the brain there is a corresponding increase in mental activity—and in this way, to a considerable extent, the functions of certain parts of the brain have been made out.

Embryology, or the study of the transitory phases through which every animal passes in its development from the stage of the egg to that of the adult, and which might be called the comparative anatomy of the individual, has already proved to be of service in throwing light on the functions of the human body, and which the future will, no doubt, show to be susceptible of even a wider application than is made of it at present, for the embryo of animals, with the exception of the lowest, consists of three germinal layers, of which the upper one gives rise to the epidermis and central nervous system, the lower one to the epithelium of the alimentary canal and its appendages, the middle one to bone, muscle, vessel, etc. These germinal layers, even at the start, can be readily distinguished, the cells composing them being differently affected by physical and chemical influences. Some of the lower animals, for example, the hydrozoa, never get beyond this layered stage, the inner layer acting as stomach, the outer as skin. If a tissue in the adult can be shown to have been derived from one of these layers in its embryonic stage its function could almost be predicted. Indeed the whole modern pathological histology is an application of this view. The older pathologists, like Morgagni,<sup>1</sup> confined themselves to the study of the organs as affected by disease.

Bichat,<sup>2</sup> in investigating the tissues of which the organs are composed, created histology; Schleiden<sup>3</sup> first showed that vegetable tissues consist of cells, and Schwann,<sup>4</sup> following his lead, applied Schleiden's view to the tissues of animals. The embryologists, Reichert,<sup>5</sup> Kolliker,<sup>6</sup> Remak,<sup>7</sup> etc., then proved that the cells composing the tissues were the modified cells of the original mulberry mass of cells into which the egg or primitive cell segments. The obvious corollary of these generalizations followed when Virchow,<sup>8</sup> Billroth,<sup>9</sup> Paget,<sup>10</sup> Rindfleisch,<sup>11</sup> etc., showed that pathological structures were the still further modified cells composing the tissues of the organ, and that morbid growths were really physiological ones, exhibiting themselves under conditions otherwise than normal; while with the development of teratology, through the works of Geoffrey St. Hilaire,<sup>12</sup> and others, the explanation of the production of monsters *lusus naturæ* became possible. That which is pathological at one stage of growth was shown to be physiological at another; that which is normal in one animal is abnormal in another. Gradually the strict demarcation between physiology and pathology has been broken down,

<sup>1</sup> De Sedibus Morborum, 1761.

<sup>2</sup> Müller's Archiv, 1838.

<sup>3</sup> Entwicklung in Wirbelthiere, 1840.

<sup>4</sup> Entwicklung der Wirbelthiere, 1852.

<sup>5</sup> Allgemeine Pathologie, 1872.

<sup>6</sup> Pathologische Anatomie, 1873.

<sup>7</sup> Histoire Générale et Particulière des Anomalies de l'organisation, 1837.

<sup>8</sup> Anatomie Générale, 1801.

<sup>9</sup> Mikroskopische Untersuchungen, 1839.

<sup>10</sup> Entwicklung der Cephalopoden, 1844.

<sup>11</sup> Cellular Pathologie, 1854.

<sup>12</sup> Surgical Pathology, 1870.



and, with the fusion of the two studies, a rational pathology and rational treatment are being slowly developed.

Notwithstanding the importance of a knowledge of general physics and chemistry, anatomy, embryology, and pathology in the study of the functions of the human body, nevertheless, the study of human physiology is often almost entirely based on experiments made upon living animals: the study of the circulation and respiration by means of the graphic method, the making of gastric fistulæ, the introduction into the system of an animal of various substances, toxic and narcotic, the removal of various parts of the nervous system, are examples of the kind of work often exclusively done in physiological laboratories.

The student of physiology, however, should not confine himself to the experimental methods, however invaluable and indispensable they may be as a means of investigation, but should avail himself, as far as possible, of the other methods of research just referred to, studying the subject from all the different points of view possible and comparing the results obtained by the various methods made use of.

As objections are often made to the experimental study of physiology, it will not, I hope, be considered superfluous if I, for a moment, consider some of the most important of those usually advanced. It is often urged as an objection to a vivisection, that the pain inflicted so disturbs the normal condition that any result as to the function of a part determined in this way is valueless; the suffering entailed vitiating any conclusion as to the healthy function of the part examined. This objection is, of course, not made if anæsthetics are used. There are, however, experiments performed in which it is necessary that the animal should be in the full possession of its faculties and which, from the conditions of the investigations, make the use of anæsthetics impossible. As regards such investigations it may be said, without doubt, that animals suffer far less from the pain inflicted in a vivisection than man does from a similar wound due to an accident or the knife of the surgeon. This is due to several causes; the animal is in ignorance of what is going to be done, forgets the operation almost immediately, his nervous organization is less susceptible than that of the human being, and his wounds heal up more quickly. The influence of pain, though less in an animal than man, must nevertheless be always taken into consideration.

Whenever the vivisection is performed without an anæsthetic, the physiologist ought not to draw any conclusion from the experiment until the animal has had time to recover from the effects of the shock, hemorrhage, etc., and has so far returned to his normal condition that the influence of pain, if any still exists, is so small in amount that it cannot be considered as interfering with the function of the structure examined. It is evident, therefore, that if the physiologist had no higher motive, selfishness would induce him to be as merciful as possible and to eliminate, so far as he is able, pain, as a possible source of fallacy in his conclusions.

The animal, both during and after vivisection, should be treated just as a patient undergoing an operation would be by a wise surgeon; the object in both cases being to restore, as rapidly as possible, the physiological conditions—the conditions of health. As an illustration of what



has just been said, as regards the amount of permanent disturbance produced in an animal by a vivisection, let me mention that Blondlot's pointer dog, in which a gastric fistula had been made, was used, after her recovery, by her master for eight years in the field for hunting purposes, and in the laboratory for obtaining gastric juice, and that during that period the dog had two litters of pups.

The Canadian St. Martin, on whom the gastric fistula was caused by a gunshot wound, producing far more dangerous effects than the vivisection just referred to, lived to be eighty-four years old, enjoyed good health all his life, married and had children, performed the duties of a servant, and was during this time frequently of inestimable value to science, as affording Dr. Beaumont and others the rare opportunity of observing gastric digestion in man under the most favorable circumstances.

One might as well object that the pain suffered by St. Martin, after the explosion of the gun, vitiated the conclusions drawn by Beaumont, as to object to the conclusions of Blondlot because the making of a gastric fistula in a dog involved the giving of the animal pain. A far more important objection than that just referred to is that, as animals differ very much in their organization, conclusions drawn from experiments made upon one kind of an animal cannot be applied to another kind; digestion in a dog, for example, not being exactly the same as in a man.

It is undoubtedly true that, while frogs, turtles, pigeons, rabbits, dogs, horses, etc., agree anatomically in many respects with each other and man, they disagree to such an extent that the result of experiments made upon one of these animals is often utterly inapplicable to the other, and entirely worthless as applied to man. Indeed, the most striking differences in the effect of certain substances are observed even in closely allied animals, varieties of the same species. Thus the black rhinoceros feeds upon the euphorbia, which poisons the white species; goats and lambs avoid most of the solanaceous plants; the ox and the rabbit will eat belladonna; the goat, the hemlock; the horse, aconite.

Such differences should be always taken into consideration when the results of a vivisection upon one animal are to be applied to the determination of the function of a structure in another. It must be always proved that the structure and functions compared are homologous. Further, a careful post-mortem examination should be always made after the vivisection, in order to learn exactly what has been done, to show that no structure has been involved which would modify the results except the one examined. It is the neglect of such precautions, the indifference to the infliction of pain, the comparing of utterly unlike conditions, the absence of the test of post-mortem examination, the want of controlling experiments, and of comparison of the results obtained with the facts of pathology and comparative anatomy that has brought vivisection into the disrepute in which it is held at the present day by many even educated persons. Crude generalizations, based upon imperfect experiments performed upon animals illogically applied to man, have made even medical men doubt altogether of the efficiency of this method, and account for their sympathizing with the well-meaning, no

doubt, but ill-judged efforts to suppress experimental investigation altogether; and yet if vivisection should be banished from the laboratory, the physiologist would be deprived of one of his most fertile methods of research. The history of physiology proves not only the importance of vivisection, but its indispensability as a means of present research. Indeed, it is no exaggeration to say that there is not an organ in the human body whose functions have not been learned, in part at least, by vivisections. Let me illustrate this statement by a few examples.

Consider the history of the circulation of the blood, and we shall see that every important advance made in a knowledge of the phenomena was due to a vivisection. Thus, Galen demonstrated by vivisection that the artery contained blood and not air, as its etymology would indicate. It was by a vivisection that Harvey proved that the blood flowed from the heart to the periphery through the arteries, and from the periphery back to the heart through the veins. Finally, it was through a vivisection that Malpighi saw, for the first time, the blood actually flowing from the arteries into the veins through the intermediate vessels, the capillaries. One of the most important discoveries ever made in physiology, that of the functions of the roots of the spinal nerves, that the anterior are motor and the posterior are sensory, was demonstrated by Majendie upon a living animal. The influence of the nervous system upon the heart, so far as is known, has been entirely learned by the experimental investigations made upon animals by the Webers, Von Bezold, Ludwig, Cyon, etc. The beautiful investigations of Bernard upon the salivary glands, the pancreas, the liver, by means of vivisections, have demonstrated certain peculiarities in reference to the secretion of these organs, that could never have been learned by any other method. By means of vivisection Brown-Séquard showed the influence of the sympathetic nerve in diminishing the calibre of the bloodvessels, and thence discovered the vasomotor nerves, by which the distribution of the blood to the tissues is regulated. It is needless to multiply examples of the importance of vivisection as a means of research, as nearly every chapter in this work will afford such. It must not be forgotten, however, that vivisection is but one means of physiological research, and that however important may be the results obtained by it, the latter, as already mentioned, should be always compared with such facts of comparative anatomy and pathology as have a bearing upon the function investigated, so that so far as possible all sources of fallacy may be eliminated.

To those familiar with the history of medicine any argument to prove the importance of the study of physiology would be superfluous. Physiology has always been, and is still, the corner-stone of medicine. The doctrines of Hippocrates, Galen, Sydenham, Boerhave, Hunter, and Virchow, reflect as a mirror the physiology of the day. It is self-evident that to understand disease and its cure one must first understand health. The study of physiology must precede that of pathology and therapeutics. Hand in hand they advance together, the progress of the one depending upon that of the other. There is no better illustration of the truth of this view of the dependence of pathology and therapeutics upon physiology than ophthalmic medicine, the most developed and



finished of all branches of medicine, whose present perfected condition is entirely due to the comparatively thorough understanding of the structure and function of the healthy eye.

On the other hand, diseases, like those of the nervous system, are in a proportionally backward condition owing to the imperfect knowledge of the normal anatomy and physiology of the parts involved.

Having defined the subject of physiology, considered the methods by which it is studied, and its importance to medicine, it only remains now in conclusion to indicate, generally, the order in which the study will be pursued, and here nature will be our guide. Our first sensations are those of hunger and thirst—hence the taking of food. We will, therefore, after describing the general physical and chemical structure of the body, begin with the study of digestion and absorption, the elaboration of the food into the blood, and its circulation will be then described, the consideration of excretion, animal heat, completing the study of nutrition.

But man is more than a vegetable, he feels, thinks, moves. Impressions of the outer world made upon his nervous system awaken in him consciousness, the inner world of mind. Through his nervous system man not only becomes aware of the existence of an environment, but adjusts his actions with reference to it. Finally, though the individual perishes in the reproduction of his kind, the race, temporarily at least, survives, hence the study of development. We will begin, therefore, with the study of nutrition, consider next the nervous system, concluding with an account of reproduction.



## CHAPTER I.

### GENERAL STRUCTURE OF THE BODY, PHYSICALLY AND CHEMICALLY.

BEFORE taking up the study of the functions, specifically, it will be well to consider, from a general point of view, of what the human body consists, physically and chemically speaking, to obtain some general knowledge of its organization, of which the functions are the living expression.

As is known to every one, the human body, like that of a domestic animal, is made up of skin, muscles, bone; of various viscera, such as the heart, lungs, liver, stomach; of nerves, arteries, etc.

The old anatomists busied themselves almost entirely with the description of such organs, their number, size, color, relative position, etc. This kind of study may be said to have culminated in Cuvier, who, as regards the exactness, extent, and variety of his knowledge stands without a rival as an anatomist. If, however, any one organ is examined somewhat closely, it will be found to be far from homogeneous. Thus the stomach consists of several layers, mucous, fibrous, muscular, etc.; the heart, of muscular, connective, adipose, nervous tissue, etc. Such tissues, combined in greater or less proportions, make up the different organs of which the body is composed; the same tissue, for example, the connective, being found in different organs, just as the substance wood may be applied to making a chair, sofa, bed, or bookcase furnishing a room.

The investigation of the tissues, the creation of histology, is due to the genius of Bichat. If now any tissue be studied in detail, it can be still further resolved into simpler ultimate physical elements or what are commonly called cells, or their modifications. This last analysis was made by Schleiden and Schwann. Through the progress of organic chemistry it has also become possible to state, with tolerable accuracy, of what the body is composed chemically. When the analysis is a proximate one, the result gives such principles as water, common salt, salts of lime; starch, sugar, fat; albumen, fibrin, casein, etc. These principles exist as such in the human body, and are called proximate principles, being the result of a proximate analysis. If now these principles be analyzed, they will be found to consist of hydrogen, oxygen, sodium, chlorine, carbon, nitrogen, phosphorus, etc. In this way it is shown that the human body consists, ultimately, of the ordinary chemical elements. A human being then consists, ultimately, of myriads of cells composed of the ordinary chemical elements. Certain cells form tissues, certain tissues act together as organs, and the organs harmoniously working together constitute a living, healthy man. The chem-

ical elements composing the cells also act in concert, as proximate principles. A *résumé* of the above physical and chemical facts may be seen thrown together synoptically under Table II.

TABLE II.<sup>1</sup>—THE HUMAN BODY CONSISTS

| PHYSICALLY.                                                                                                             | CHEMICALLY                                                                                                                         |
|-------------------------------------------------------------------------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------|
| <i>of Organs.</i>                                                                                                       | <i>of Principles.</i>                                                                                                              |
| The organs of tissues.                                                                                                  | The principles of elements.<br>Proximate principles.                                                                               |
| The tissues of cells.                                                                                                   |                                                                                                                                    |
| The cells of elements.                                                                                                  |                                                                                                                                    |
| <i>Examples of Cells.</i>                                                                                               | <i>of 1st Class.</i>                                                                                                               |
| 1. Cells floating in a liquid: blood corpuscles, lymph corpuscles.                                                      | Water, sodium chloride, calcium phosphate, calcium carbonate, etc.                                                                 |
| 2. Cells in layers: epidermis, epithelium, enamel.                                                                      |                                                                                                                                    |
| 3. Cells in masses: adipose tissue, medulla of hair.                                                                    | <i>of 2d Class.</i>                                                                                                                |
| 4. Cells imbedded in non-cellular substance: cartilage, bone.                                                           | Starch, sugar, oils, fats.                                                                                                         |
| 5. Cells forming fusiform bands: unstriated muscular fibre.                                                             |                                                                                                                                    |
| 6. Cells transformed into tubes: capillaries, nerves, dentine.                                                          | <i>of 3d Class.</i>                                                                                                                |
| 7. Cells transformed into filaments: fibrous tissue, elastic tissue.                                                    | Albumen, fibrin, casein, etc.                                                                                                      |
| A cell may consist, in its wall, of membrane; in its contents, of liquid and granules; in its appendages, of filaments. |                                                                                                                                    |
|                                                                                                                         | <i>Ultimate Elements.</i>                                                                                                          |
|                                                                                                                         | Oxygen, hydrogen, carbon, nitrogen, chlorine, phosphorus, sulphur, calcium, sodium, potassium, magnesium, iron, fluorine, silicon. |

Let me now take up somewhat more in detail what is known of cells and proximate principles. A cell may be defined as the ultimate elementary living unit, a mass of living matter, varying from the  $\frac{1}{5000}$ th to the  $\frac{1}{120}$ th of an inch in diameter. It may consist of a cell wall, inclosing cell contents of a liquid, semi-liquid, or granular character. The granules in some cells are united, according to many histologists, by filaments or threads; the cell contents consisting then of a network. Often among the cell contents can be distinguished a still smaller cell, the nucleus, and, within this, the nucleolus. Sometimes the cell wall is elongated into an appendage, a *cilium*. Great difference still prevails, as may be seen from the views of Kölliker, Leydig, Schultze, Brücke, Hæckel, Gegenbaur, Beale, etc., as to the relative importance of the nucleus and nucleolus of the cell contents and cell wall.

According to some observers, the all important element in cell life is the nucleus, while others maintain that it is the cell contents. The cell wall and even the nucleus are regarded by some as the cell contents in a state of retrograde metamorphosis.

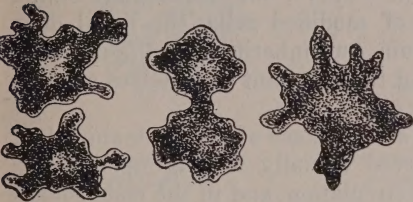
As we proceed in our studies, it will be seen that there are cells, like

<sup>1</sup> Partly taken from Leidy's Anatomy, p. 32.



the blood corpuscles, which have neither nucleus nor cell wall; that the first step in the division of the egg or primitive cell consists in the disappearance of the germinal vesicle or nucleus, and that the mulberry mass of cells, the result of that division, are at first without a cell wall. Further, there are protoplasmic beings, like the monera, of which the protamoeba (Fig. 1) is an example which, through life, never exhibit either

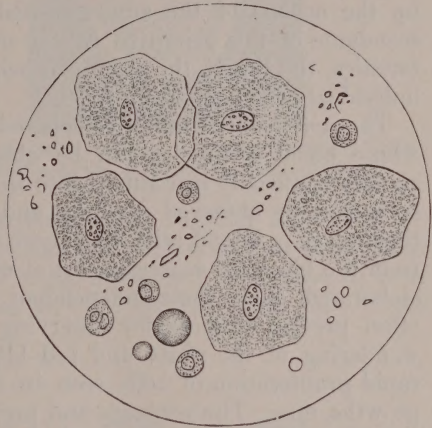
FIG. 1.



Protamoeba. (HÄCKEL.)

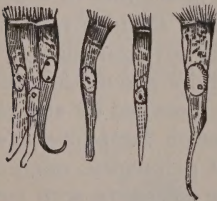
nucleus or cell wall. Such facts prove that in certain cases, at least, neither the nucleus nor cell wall is an indispensable element to the life of cells, and should make physiologists cautious in attributing positive functions to this or that element of a cell. Indeed, I cannot say that the relative significance of either nucleus, nucleolus, cell wall, or cell contents, is as yet definitely understood. As examples of cells, attention may be called to those lining the

FIG. 2.



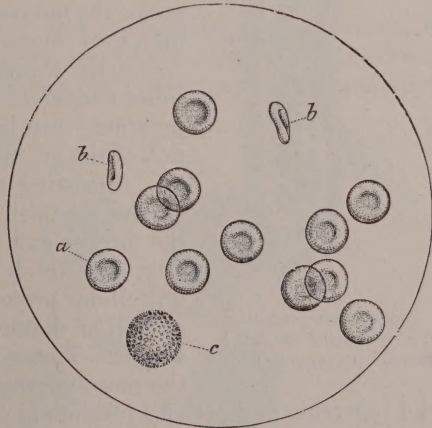
Buccal and glandular epithelium, with granular matter and oil-globules; deposited as sediment from human saliva. (DALTON.)

FIG. 3.



Columnar ciliated epithelium cells from the human nasal membrane; magnified 300 diameters. (QUAIN and SHARPEY.)

FIG. 4.



Human blood-globules. a. Red globules, seen flatwise. b. Red globules, seen edgewise. c. White globule. (DALTON.)

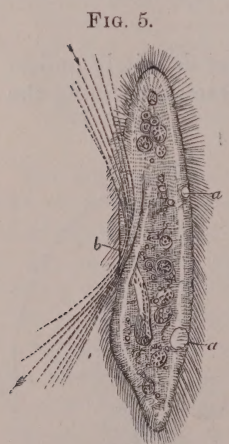
uriniferous tubules of the kidney, to the cells of the enamel, to those of the epithelium of the mouth (Fig. 2), of the columnar epithelium of the intestine, to the multipolar cell found in nervous tissues, to the ciliated epithelial cells from the pulmonary mucous membrane (Fig. 3), to blood cells (Fig. 4), to unstriated muscular fibre cells.

As I take up the different organs, the cells composing their tissues will be described more in detail; so the above examples will, therefore, suffice for the present in giving a general idea of the form of cells.

While there is still some doubt as to the exact use of the different parts of the cells, there is no doubt that the life of the organism resides in the cells composing it. Among other reasons for supposing so, may be mentioned the fact that the life of the human being begins as the ovum, a cell, and that the tissues of the embryo, out of which are built up the organs of the adult, consist of modified cells, the lineal descendants of this primitive cell or ovum, and inheriting its life characteristics, the life of the organism being the resultant of the lives of the individual cells composing it.

The independent life of cells is well seen in some of the lower animals, whose blood corpuscles can be observed actually feeding upon substances artificially introduced into the circulation, and in the embryonic state can be observed dividing and subdividing, and so reproducing themselves. Gland cells, like those of the liver, kidney, etc., in taking from the blood the materials out of which their respective secretions are elaborated, show their independent activities. Pathological processes often present chances for observing this independent cell life, in the wandering of the white and red blood-cells out of the vessels, in the rapid proliferation of cells seen in the development of various morbid growths, etc. The protozoa and protophyta, or the simplest of animals and plants, however, offer the most favorable opportunities for observing

the life history of cells; for these simple beings never get beyond the one-cell stage of life, indeed neither tissues nor organs are ever developed in them in the same sense that these are in the higher animals. The entire life cycle of these minute plants and animals can be often followed under the microscope. The manner in which cells take food, move about, their mode of reproduction—usually through simple division, though sometimes endogeneously and by gemmation and conjugation—can be readily observed by an examination of the greenish matter on damp bricks, stones, etc., consisting usually of palmoglea, micrococcus, or the greenish film-like spirogyra seen covering the ditches and ponds in the neighborhood of the city, and which also usually contain specimens of unicellular protozoa paramœcium (Fig. 5), stentor, as well as desmidiaceæ, of which Fig. 6 is an example. These researches, always interesting to the mere microscopist on account of the beauty of



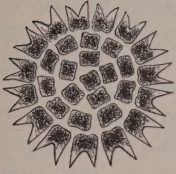
Paramœcium caudatum.  
a, a. Contractile vesicles. b.  
Mouth. (CARPENTER.)

the vegetable and activity of the animal forms, have a deep meaning to the philosophical physiologist. For it is reasonable to suppose that the life of man or the higher animals, when in the one-cell or ovum stage (Fig. 7), is similar to that of these beings which pass beyond this unicellular stage. Hence, we may conclude that the human ovum, or any of the cells descended from it, absorbs and assimilates nutriment, like



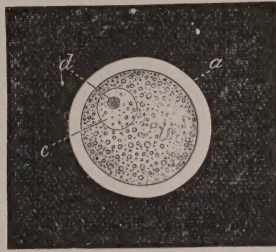
the unicellular beings just referred to. The segmentation of the egg in the higher animals corresponds also to the division of the cell seen in

FIG. 6.



Pediatrum pertusum.  
(CARPENTER.)

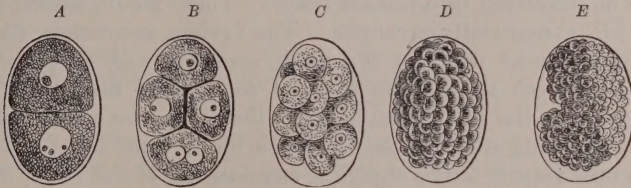
FIG. 7.



Human ovum, magnified 85 diam. a. Vitelline membrane. b. Vitellus. c. Germinative vesicle. d. Germinative spot. (DALTON.)

the reproduction of these minute beings, the manner in which the nucleus divides first into two halves and the cell contents or protoplasm constricts around the new nuclei being essentially the same in both cases; the only difference being, as we shall see hereafter, that in the

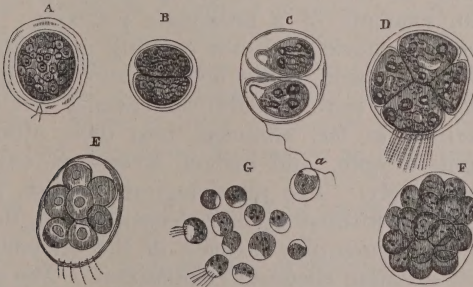
FIG. 8.



Division of the yolk of Ascaris. A, B, C (from K lliker), ovum of Ascaris nigrovenosa; D and E, that of Ascaris acuminata (from Bagge). (QUAIN and SHARPEY.)

former the new cells hold together and are transformed into tissue, in the latter the new cells are scattered, constituting the next generation of cells. This distinction may be seen by comparing the segmentation

FIG. 9.



Development of protococcus pluvialis. (CARPENTER.)

of ascaris (Fig. 8) with the reproduction of protococcus through continued subdivision (Fig. 9). In either case, however, the life of the re-

sultant cells is that inherited by them from the parent cell. The cells resulting from the segmentation of the mammalian ovum or egg are at first very similar, but soon a marked difference between them can be observed. If the researches of Van Beneden<sup>1</sup> on the rabbit are confirmed, the difference is noticeable even in the two first segmentation cells. However this may be, the cells soon begin to differ in size, shape, and the manner in which they are affected by chemical agents. Some dispose themselves so as to form the epiblast, others the hypoblast, and between these two layers a third appears, the mesoblast.

The modification of the cells and the further development of these three layers will be considered when I take up the subject of reproduction. It will be seen then that through the processes incidental to development, cells often lose their originally round form, becoming sometimes flattened or scale-like, and often of a prismatic and columnar shape. Sometimes the cells float free in a liquid, like the blood corpuscles; or they may arrange themselves in layers, like those of the enamel; or in masses, as seen in the medulla of hairs. They may be imbedded in a solid non-cellular matrix, as in cartilage. Cells are sometimes flattened into bands, as in the unstriated muscular fibre, or a number are, through the dissolution of their adjacent walls, metamorphosed into tubes, of which the capillaries and dentine are examples, or they may be converted into fibrous tissue. These modifications are seen in Table II., synoptically arranged. The various substances elaborated by cells in different parts of the adult economy will be more appropriately considered as the functions of the organs are taken up. It will be seen that the life of the body is, therefore, the resultant life of the cells composing it; that the body is a living republic of cells.

Let us now return to the chemical composition of the body, or of the cells of which it consists. We have seen that the human body consists of chemical elements acting as proximate principles. Before considering these, let us see what is meant by a proximate principle.

A proximate principle may be defined as a principle, simple or compound, which exists and acts as such in the human body. Thus, sodium chloride is a proximate principle. Neither the rare metal sodium, nor the offensive greenish gas chlorine, however, are proximate principles, for they do not exist or act as such in the body. Calcium phosphate is an example of a proximate principle; but the metal calcium, and the phosphoric acid, not existing or acting separately, as calcium and phosphoric acid, in the body, cannot be regarded as proximate principles. The purely analytical chemist would resolve such proximate principles as fat, albumen, into their ultimate elements, carbon, hydrogen, oxygen, and carbon, hydrogen, oxygen, nitrogen, phosphorus, respectively. The physiological chemist, however, would study these principles without further decomposition, investigating the part that fat and albumen play as such in the economy, without any reference to their ultimate chemical composition. The proximate principles—leaving out of consideration, for the present, the gases, which can be more conveniently treated of under the subjects of respiration

<sup>1</sup> Bulletin de l'Acad. Belgique, 1874.



and the blood, and the various effete matters whose elimination from the economy constitutes the function—divide themselves naturally into those of inorganic and organic origin; the latter are further distinguished by those containing nitrogen and those which do not. Table II. gives some typical examples of these three classes of the proximate principles; and of their ultimate chemical elements, manganese, iodine, and bromine, though not existing in man, have been found, however, in other organized bodies.

By referring to Tables III. and IX. a list of the most important of the proximate principles may be seen, and the parts of the body in which they usually occur. Let me now take up somewhat in detail the consideration of these principles, beginning with those of inorganic origin.

TABLE III.<sup>1</sup>—PROXIMATE PRINCIPLES OF THE FIRST CLASS, OR THOSE OF INORGANIC ORIGIN.

| Substances.                   | Where found.                                       |
|-------------------------------|----------------------------------------------------|
| Water . . . . .               | Universal.                                         |
| Sodium chloride . . . . .     | Universal, except enamel.                          |
| Potassium chloride . . . . .  | Muscles, blood, milk, saliva, bile, gastric juice. |
| Calcium phosphate . . . . .   | Universal.                                         |
| Calcium carbonate . . . . .   | Bones, teeth, cartilage.                           |
| Sodium carbonate . . . . .    | Blood, saliva, lymph.                              |
| Potassium carbonate . . . . . | Bones, lymph.                                      |
| Magnesium phosphate . . . . . | Universal.                                         |
| Sodium phosphate . . . . .    | Universal.                                         |
| Potassium phosphate . . . . . | Universal.                                         |
| Sodium sulphate . . . . .     | Universal, except milk.                            |
| Potassium sulphate . . . . .  | Bile, gastric juice. Same as sodium sulphate.      |
| Calcium sulphate . . . . .    | Blood, feces.                                      |
| Ammonium chloride . . . . .   | Gastric juice, saliva, tears.                      |
| Magnesium carbonate . . . . . | Blood, sebaceous matter.                           |
| Sodium bicarbonate . . . . .  | Blood.                                             |

As implied in the definition, the principles of this class are inorganic in origin, being found in the rocks forming the crust of the earth, in sea water, springs, etc. They have a definite chemical composition, and are crystallizable. With the exception of calcium carbonate, of which the otoliths of the ear consist, they are combined in the body with the organic principles. This union is so intimate that as the organic principles become effete, and are eliminated, the inorganic substances are cast out with them. Some of these substances play a more important rôle than others, and are found in greater or less quantities in the economy.

Let us consider now the most important of these substances, where they occur, and their principal uses.

WATER,  $H_2O$ .—In the maintenance of life, none of the proximate principles, whether inorganic or organic, surpass in importance water. When it is learned, however, that it constitutes nearly three-fifths by weight of the whole body, this will no longer be a subject of surprise.

<sup>1</sup> Robin et Verdeil: *Traité de Chimie Anatomique*, tome deuxième, p. 5. Paris, 1853.

In the course of our studies we shall find that water exists in all parts of the body: in solids, like bone and enamel; in fluids, like the tears, perspiration, etc. Its uses in the economy are manifold. It gives consistence and general resiliency to the body, pliability to tendons, elasticity to cartilage, resistance to the bones. Various substances, like articles of food and the effete matters, find their way into and out of the body through their solubility in water. The importance of water is at once seen if the system is deprived of it. The tissues become shrivelled and dried up and inflexible, the liquids become thick, inspissated, lose their fluidity. On the other hand, an excess of water gives rise to general debility, muscular weakness, dropsies, etc.

In the living body water exists as "water of composition"—that is, it constitutes an integral part of the tissues. The water is not taken up by the tissues, like a sponge, but really forms a part of its substance, the union being a chemical one.

TABLE IV.<sup>1</sup>—QUANTITY OF WATER.

| Substance.           | Parts per 1000. | Substance.                | Parts per 1000. |
|----------------------|-----------------|---------------------------|-----------------|
| Enamel . . . . .     | 2               | Milk . . . . .            | 887             |
| Epithelium . . . . . | 37              | Chyle . . . . .           | 904             |
| Teeth . . . . .      | 100             | Bile . . . . .            | 905             |
| Bones . . . . .      | 130             | Urine . . . . .           | 933             |
| Tendons . . . . .    | 500             | Lymph . . . . .           | 960             |
| Cartilages . . . . . | 550             | Saliva . . . . .          | 983             |
| Skin . . . . .       | 575             | Gastric juice . . . . .   | 984             |
| Liver . . . . .      | 618             | Perspiration . . . . .    | 986             |
| Muscles . . . . .    | 725             | Tears . . . . .           | 990             |
| Ligaments . . . . .  | 768             | Pulmonary vapor . . . . . | 997             |
| Blood . . . . .      | 780             |                           |                 |

The relative amount of water is, in the tissues, regulated by the salts. Thus, when water is added to the blood, the corpuscles become swollen, and finally are dissolved away; but if a strong solution of salt be added instead, the corpuscles lose their water and shrivel up. Most of the water found in the system is taken in as part of the solid and fluid articles of the food. As we shall see hereafter, however, about 500 grammes, or 7500 grains, are formed in the system through the combustion of carbohydrates. The daily amount of water necessary for the healthy adult has been estimated, by Dalton,<sup>2</sup> at about four and one-half pounds. This, of course, includes the water entering into the solid articles of food. About fifty-two per cent. of the water, after it has played its part in the economy, is discharged by the skin and lungs, the rest by the kidneys and with the feces. It has been calculated that nearly one pound passes off by the skin, about a pound by the lungs, and a little over three pounds by the kidneys. When, however, the skin is not active, as in the winter time, then the kidneys act very freely; in the summer the reverse is the case. Diuretics favor the one set of emunctories, diaphoretics the other.

By glancing at Table IV. it may be seen how universally water is found in the tissues, and its relative amount. Thus, while we find that

<sup>1</sup> Robin et Verdeil, *op. cit.*, p. 115.<sup>2</sup> Physiology.



a thousand parts of pulmonary vapor contain nine hundred and ninety-seven parts of water, it will be seen there are only two parts of water in a thousand of enamel, and that a substance, like tendon, so different from either of those just mentioned, is half made up of water. The great importance of water in health, and still more in disease, cannot be too much dwelt upon by the physiologist and practising physician.

**SODIUM CHLORIDE, NaCl.**—Next to water, common salt is the most important of the inorganic proximate principles, being found, like water, almost universally, even in the ovum. With the exception of the enamel, in which it has not yet been discovered, salt is found in all the solids and fluids of the body. The absolute amount, however, has not yet been determined. The saltish taste of the tears and perspiration is due to the presence of this principle. It is found in the largest proportion in fluids. The relative quantity of sodium chloride found in some of the fluids of the body may be seen by looking at Table V.

TABLE V.<sup>1</sup>—QUANTITY OF SODIUM CHLORIDE.

| Substance.      | Parts per 1000. | Substance.             | Parts per 1000. |
|-----------------|-----------------|------------------------|-----------------|
| Blood . . . . . | 4.2             | Saliva . . . . .       | 1.5             |
| Chyle . . . . . | 5.3             | Perspiration . . . . . | 3.4             |
| Lymph . . . . . | 4.1             | Urine . . . . .        | 4.4             |
| Milk . . . . .  | 0.8             | Feces . . . . .        | 3.0             |

Salt is introduced into the system through the different articles of animal and vegetable food which always contain it; in addition, salt as such is added to the food of man and the herbivora; the amount contained in their food not being sufficient for the wants of the economy. Salt, like all other inorganic principles, passes ultimately through the body, and is carried out of it in the urine, feces, perspiration, etc. The uses of salt in the system are manifold. The phenomena of osmosis, or the passage of fluids and gases through the animal membranes, are greatly modified by the amount of salt present, a solution of salt osmosing through a membrane much less readily than pure water. Absorption is influenced by it. It increases the solubility of albumen; this principle being coagulated much less quickly by heat in a solution of sodium chloride than in water. The coagulability of fibrin may be prevented by a strong saline solution. The forms of tissues are preserved through the presence of salt, as in the case of blood-corpuscles just referred to. Nutrition is undoubtedly affected in other ways by salt, as yet not perfectly understood. The experiments of Boussingault<sup>2</sup> upon bullocks, and of Dailly<sup>3</sup> upon sheep, showed what a deleterious effect was produced in their general appearance when these animals were deprived of salt. It is well known how the wild buffalo is found by the salt licks of the Northwest, and how the hunter in Southern Africa avails himself of his knowledge of the habits of wild animals collecting near salt springs, to kill his game. Every one is familiar with the fact of how cattle run to any one who will give them salt. It is said that fugitives from justice will often risk capture and their lives to obtain salt. Facts like the

<sup>1</sup> Robin et Verdeil, op. cit., p. 176.<sup>2</sup> Chimie Agricole, p. 271. Paris, 1854.<sup>3</sup> Longet: Traité de Physiologie, tome i. p. 76.

above show what a deep-seated want is felt by man and beast alike, when deprived of salt.

**POTASSIUM CHLORIDE, KCl.**—This principle is found in the muscles, blood, saliva, bile, gastric juice, urine, etc. A greater part of it is introduced into the system with the food, though probably some is produced through the double decomposition of the potassium phosphate and sodium chloride existing in the blood, sodium phosphate and potassium chloride resulting. The uses of potassium chloride and sodium chloride are probably the same in the economy. This principle is discharged from the body in the mucus and the urine.

**CALCIUM PHOSPHATE,  $\text{Ca}_3(\text{PO}_4)_2$ .**—This very important principle is found in all the solids and fluids of the body. By looking at Table VI. it will be seen, however, that calcium phosphate exists in much larger proportions in the solids than in the fluids. Only traces are found in blood, saliva, etc., whereas a thousand parts of enamel will contain nearly nine hundred parts of this principle. Calcium phosphate, while insoluble in water, is held in solution in certain parts of the system by the free carbonic acid, the bicarbonates and the sodium chloride—in the urine, for example, by the acid sodium phosphate. On the other hand, this principle is in a solid condition in bones, teeth, cartilage, etc. Calcium phosphate forms one of the ingredients of our food and so gets into the system; it is eliminated in the feces and urine. Its use in the economy is to give strength and solidity. Hence the large amount present in the bones, and more especially in the enamel, the hardest of all known organic substances. It is very abundant in the lower extremities, which support the weight of the body. The ribs contain less calcium phosphate than the upper extremities, hence their greater elasticity.

TABLE VI.<sup>1</sup>—QUANTITY OF CALCIUM PHOSPHATE.

| Substance.           | Parts per 1000. | Substance.                         | Parts per 1000. |
|----------------------|-----------------|------------------------------------|-----------------|
| Blood . . . . .      | 0.7             | Teeth of infant . . . . .          | 510.0           |
| Milk . . . . .       | 2.5             | Teeth of adult . . . . .           | 610.0           |
| Saliva . . . . .     | 0.6             | Teeth of man at 81 years . . . . . | 660.0           |
| Urine . . . . .      | 25.0            | Enamel . . . . .                   | 885.0           |
| Excrements . . . . . | 40.0            | Rachitic bone . . . . .            | 136.0           |
| Bone . . . . .       | 400.0           |                                    |                 |

The amount of calcium phosphate found in any organ or tissue differs often according to age; thus it will be seen from Table VI. that in the teeth of a very old man, in a thousand parts there are one hundred and fifty parts more than in an infant, and fifty more than in an adult. Rickets is due to a want of the proper amount of calcium phosphate. The liability of pregnant women to meet with fractures, and the delay of union in these cases, are due to their offspring taking from the mother so much calcium phosphate, necessary in the development of the new being. The calcium phosphate in a bone can be all dissolved out by hydrochloric acid; such a bone retains its form, but if it be the fibula, is so pliable that it can be tied in a knot, a good illustration of the importance of this salt to the system. If animals be deprived of their proper

<sup>1</sup> Robin et Verdeil, op. cit., p. 287.



amount of calcium phosphate their bones soften, as seen in Chossat's experiments on pigeons.

**CALCIUM CARBONATE,  $\text{CaCO}_3$ .**—This principle is found in the blood, teeth, cartilage, and bones. In the latter it is not as abundant as the phosphate, but exists in the proportion of a hundred parts to the thousand (see Table VII.).

TABLE VII.<sup>1</sup>—QUANTITY OF CALCIUM CARBONATE.

| Substance.                                 | Parts per 1000. |
|--------------------------------------------|-----------------|
| Bone . . . . .                             | 102.0           |
| Teeth of infant . . . . .                  | 140 0           |
| Teeth of adult . . . . .                   | 100.0           |
| Teeth of man at eighty-one years . . . . . | 10.0            |

As before mentioned, calcium carbonate is the only inorganic principle which exists in a crystalline form and uncombined in the body. As such, it is found in the otoliths of the internal ear. Calcium carbonate is found in our food, and in this way is introduced into the system. It is held in solution by carbonic acid. Some of the calcium carbonate found in the system is no doubt due to the decomposition of the malates, citrates, tartrates, acetates present in the food, into carbonic acid. It passes out of the body in the urine, probably transformed into the phosphate. The uses of calcium carbonate in the economy are the same essentially as those of the phosphate.

**SODIUM CARBONATE,  $\text{Na}_2\text{CO}_3$ .**—Sodium carbonate is found (Table VIII.) in the blood, saliva, etc., the alkalinity of these fluids being due to its presence. It is not introduced from without, but is formed in the system through the decomposition into carbonic acid, of the malates, tartrates, etc., found in fruits. Some of it occasionally passes away in the urine, but a greater part is decomposed by the acid of the lungs; the carbonic acid set free being exhaled.

TABLE VIII.<sup>2</sup>—QUANTITY OF SODIUM CARBONATE.

| Substance.                       | Parts per 1000. |
|----------------------------------|-----------------|
| Blood . . . . .                  | 1.6             |
| Lymph. . . . .                   | 0.5             |
| Cephalo fluid . . . . .          | 0.6             |
| Compact tissue of bone . . . . . | 2.0             |
| Spongy tissue of bone . . . . .  | 0.7             |

Sodium carbonate seems to maintain the albumen and fibrin of the blood in a fluid condition, and is of use also in preserving the form of the blood corpuscles. What has just been said of sodium carbonate applies equally well to potassium carbonate ( $\text{K}_2\text{CO}_3$ ), sodium phosphate, etc.

Sodium phosphate ( $\text{Na}_2\text{HPO}_4$ ), magnesium phosphate ( $\text{MgHPO}_4$ ), and potassium phosphate ( $\text{K}_2\text{HPO}_4$ ), are found in small quantities all through the body. They exist in our food, and are discharged in the urine and feces. Their use seems to be similar to that of calcium phosphate.

<sup>1</sup> Robin et Verdeil, op. cit., p. 223.<sup>2</sup> Robin et Verdeil, op. cit., p. 258.

There are found in the blood, and some other of the fluids and solids of the body also, sodium sulphate ( $\text{Na}_2\text{SO}_4$ ), potassium sulphate ( $\text{K}_2\text{SO}_4$ ), and calcium sulphate ( $\text{CaSO}_4$ ). The first two of these salts are introduced in the food and are discharged in the urine. Their functions seem to be the same as the sodium carbonate. The calcium sulphate is found in drinking water, and is evacuated in the feces; its function is unknown. Magnesium carbonate ( $\text{MgCO}_3$ ) and sodium bicarbonate ( $\text{NaHCO}_3$ ) have been found in the blood. Finally, ammonium chloride ( $\text{NH}_4\text{Cl}$ ) is found in the tears, saliva; its origin and use are very obscure.

Some physiological chemists subdivide the inorganic proximate principles into two classes: those which appear indispensable to the constitution of the tissues, as water, calcium phosphate, etc., and those which influence the processes of nutrition without absolutely entering into the composition of the tissues, like the chlorides.

It appears to me however, that at present, at least, no such sharp lines of demarcation can be drawn between these principles. Water, for example, while existing in many tissues in a molecular state of combination, no doubt influences the processes of nutrition. On the other hand, while common salt plays an important rôle in nutrition, under certain conditions, it seems to be as much a tissue element as calcium phosphate.

In the present state of physiological chemistry, it seems premature, therefore, to draw any very fine distinctions as to the relative importance of this or that inorganic principle, or do more than point out, as I endeavored to do in a general way, their uses in the human economy.



## CHAPTER II.

### PROXIMATE PRINCIPLES OF ORGANIC ORIGIN.

As has been already stated, in addition to the inorganic proximate principles, the human body contains many of organic origin—that is, principles elaborated by organized bodies, plants, or animals; some of these principles have already been prepared artificially by chemists, and there is no reason why in time they should not all be. They naturally arrange themselves into two classes, those containing no nitrogen and those in which this principle is present. Table IX. gives some of these principles and where they are found. Let us consider the former class first.

TABLE IX.—ORGANIC PRINCIPLES,

| <i>Containing no Nitrogen.</i> |   |   |   |   |   | Where found.           |
|--------------------------------|---|---|---|---|---|------------------------|
| Substances                     |   |   |   |   |   |                        |
| Starch . . . . .               | . | . | . | . | . | Brain.                 |
| Sugar . . . . .                | . | . | . | . | . | Milk.                  |
| Fat . . . . .                  | . | . | . | . | . | Almost universal.      |
| Pneumic acid . . . . .         | . | . | . | . | . | Lungs.                 |
| <i>Containing Nitrogen.</i>    |   |   |   |   |   |                        |
| Albumen . . . . .              | . | . | . | . | . | } Blood, chyle, lymph. |
| Fibrin . . . . .               | . | . | . | . | . |                        |
| Albuminose . . . . .           | . | . | . | . | . | Chyme, blood.          |
| Casein . . . . .               | . | . | . | . | . | Milk.                  |
| Mucosin . . . . .              | . | . | . | . | . | Mucus.                 |
| Pancreatin . . . . .           | . | . | . | . | . | Pancreatic juice.      |
| Pepsin . . . . .               | . | . | . | . | . | Gastric juice.         |
| Globulin . . . . .             | . | . | . | . | . | Blood corpuscles.      |
| Musculin . . . . .             | . | . | . | . | . | Muscles.               |
| Ostein . . . . .               | . | . | . | . | . | Bone.                  |
| Cartilagin . . . . .           | . | . | . | . | . | Cartilage.             |
| Elasticin . . . . .            | . | . | . | . | . | Elastic tissue.        |
| Keratin . . . . .              | . | . | . | . | . | Nails.                 |
| Crystallin . . . . .           | . | . | . | . | . | Lens.                  |
| Hæmatin . . . . .              | . | . | . | . | . | Blood.                 |
| Melanin . . . . .              | . | . | . | . | . | Pigment.               |
| Biliverdin . . . . .           | . | . | . | . | . | Bile.                  |
| Urrosacin . . . . .            | . | . | . | . | . | Urine.                 |

NON-NITROGENOUS PRINCIPLES OF ORGANIC ORIGIN.—This class of proximate principles is represented by the starches, sugars, fats, fatty acids, and oils, lactic acid and lactates, pneumic acid and sodium pneumate; but, <sup>these</sup> as already mentioned, when not obtained artificially, are produced only by plants and animals. These substances do not form a part of the mineral world, like such principles as salt, calcium phosphate, etc., just considered. They agree with the <sup>in</sup>organic proximate <sup>these,</sup> <sup>inorganic</sup>

principles in having a definite chemical composition, and, with the exception of starch, are crystallizable. In striking contrast with the principles of the first class, with the exception of the butter and sugar of milk of lactation, those of the second class are never discharged from the body while in a state of health. The principles of the second class differ from those of the third not only in the absence of nitrogen, but, as we shall see, these latter are not crystallizable.

By glancing at Table X. it will be seen that of these principles, starch, sugar, and stearin—a form of fat, consist of carbon, hydrogen, and oxygen.

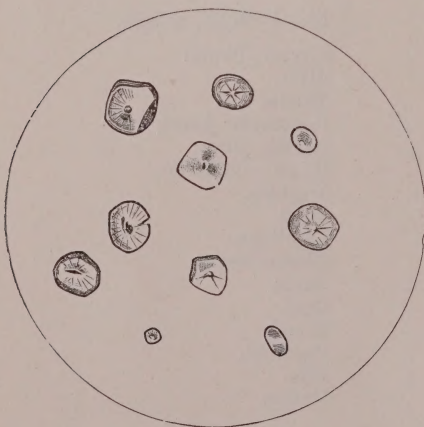
TABLE X.—COMPOSITION OF

|             |   |   |   |   |   |   |   |   |                                                                     |
|-------------|---|---|---|---|---|---|---|---|---------------------------------------------------------------------|
| Water       | . | . | . | . | . | . | . | . | H <sub>2</sub> O.                                                   |
| Starch      | . | . | . | . | . | . | . | . | C <sub>18</sub> H <sub>30</sub> O <sub>15</sub> .                   |
| Cane sugar  | . | . | . | . | . | . | . | . | C <sub>12</sub> H <sub>22</sub> O <sub>11</sub> .                   |
| Grape sugar | . | . | . | . | . | . | . | . | C <sub>6</sub> H <sub>12</sub> O <sub>6</sub> .                     |
| Stearin     | . | . | . | . | . | . | . | . | C <sub>57</sub> H <sub>110</sub> O <sub>6</sub> .                   |
| Albumen.    | . | . | . | . | . | . | . | . | C <sub>72</sub> H <sub>112</sub> O <sub>22</sub> N <sub>18</sub> S. |

These particular principles are often known as the carbohydrates. The term, however, is only applicable to the starch and sugar, since <sup>two</sup> it is only in the <sup>oxy</sup>latter that the hydrogen and oxygen exist in the proportion to form water, the hydrogen being largely in excess of the oxygen in the fats. Let us begin our study of the second class of proximate principles with starch.

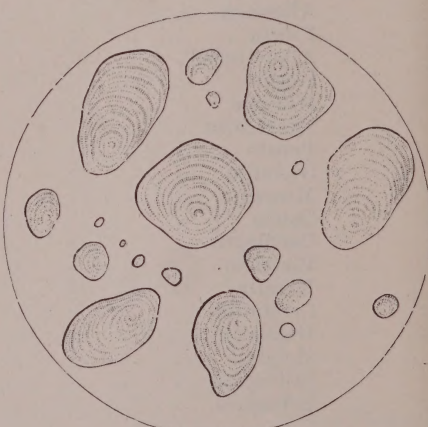
STARCH, C<sub>18</sub>H<sub>30</sub>O<sub>15</sub>.—Starch exists in the human body as the corpora amylacea, the starch granules that are found in the walls of the lateral

FIG. 10.



Starch grains from wall of lateral ventricles;  
from a woman aged thirty-five. (DALTON.)

FIG. 11.



Grains of potato starch. (DALTON.)

ventricles of the brain, in the fornix, septum lucidum, etc., described by Kölliker<sup>1</sup> and Virchow.<sup>2</sup> They resemble (Fig. 10), to a considerable

<sup>1</sup> Handbuch der Gewebelehre, 1852, S. 311.

<sup>2</sup> Cellular Pathology. Translated by Chance. 7th edit., p. 313.

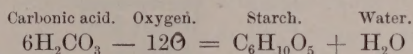


extent, the starch grains of Indian corn. They are transparent and colorless, like the starch granules of plants generally. They average about the  $\frac{1}{1800}$ th of an inch in size, present a hilus, are slightly laminated, and give the characteristic blue color when treated with iodine. Although not crystallizable, starch is far from being an amorphous powder, as seen from the above description of the corpora amylacea, but the characteristic structure of the starch granule is better seen in that of the potato (Fig. 11), where the laminations and the hilus of the granules are well marked. Starch exists abundantly (see Table XI.) in corn, wheat, oats, rice, potatoes, and indeed in almost all vegetable food. Tapioca, arrowroot, etc., so useful as articles of diet, under certain circumstances, are varieties of starch.

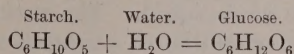
TABLE XI.<sup>1</sup>—QUANTITY OF STARCH IN 100 PARTS IN

|                       |       |                          |       |
|-----------------------|-------|--------------------------|-------|
| Rice . . . . .        | 88.65 | Peas . . . . .           | 37.30 |
| Indian corn . . . . . | 67.55 | Beans . . . . .          | 33.00 |
| Barley . . . . .      | 66.43 | Flaxseed . . . . .       | 23.40 |
| Oats . . . . .        | 60.59 | Potatoes . . . . .       | 20.00 |
| Rye . . . . .         | 64.65 | Sweet potatoes . . . . . | 16.05 |
| Wheat . . . . .       | 57.88 | Chocolate . . . . .      | 11.00 |

Whatever may be the source from which starch is derived, it is chemically the same, and is produced in growing vegetables, under the influence of solar light, by a process of deoxidation of carbonic acid, as shown by the following formula:



The principle of the development of starch through the deoxidation of carbonic acid may be roughly illustrated in the following manner: A bunch of fresh mint being placed within a cylindrical tube containing dilute carbonic acid water standing over the pneumatic trough is exposed to sunlight. Soon the leaves of the mint will be seen covered with minute beads of gas, a small quantity of the latter accumulating at the top of the cylindrical tube. By withdrawing the mint and passing up a few bubbles of nitric oxide, a dark brown vapor will appear at the top of the tube, proving that the contained gas was oxygen. Starch is insoluble in cold water, but, by boiling, the granules are liquefied, and, on cooling, remain fused together as a whitish, oxaline, homogeneous mass. In this condition, it is said to be "hydrated." The most important property of starch for the physiologist, however, is the readiness with which it is converted into sugar. This might be inferred from their relative composition, the only difference being in the amount of water (see Table X.). Thus, if human saliva be added to boiled starch and the mixture be maintained at a temperature of 100° F., in a few minutes it will be found to have been converted into sugar as shown by the following formula:



<sup>1</sup> Dalton : Physiology, 1882, p. 52. Payen : Substances Alimentaires, p. 265. Paris, 1865.

All of the starch in the food is soon converted into glucose in the alimentary canal by the digestive processes, and in this form disappears from the economy. The use of starch leads us naturally to the consideration of sugar or the form in which it appears, with the exception of the corpora amylacea, in the body.

**SUGAR.**—This principle is found in the alimentary canal during digestion, under the form of glucose,  $C_6H_{12}O_6$ , as milk sugar,  $C_{12}H_{22}O_{11} + H_2O$ , during lactation. The liver also contains glycogen,  $C_6H_{10}O_5$ , a substance readily converted into sugar, which passes into the hepatic veins, and from there to the vena cava and heart. In the muscles are found inosite,  $C_6H_{12}O_6 + 2H_2O$ , and a substance similar to grape sugar. Sugar exists in the economy combined with other proximate principles. Thus, in the blood we find the sugar dissolved in water combined with the albumen, sodium chloride, etc.

These animal sugars are closely related, chemically, and are readily converted into one another. While sugar is produced in man by the liver and mammary glands, etc., by far the greater part is derived from the food either in the form of cane sugar,  $C_{12}H_{22}O_{11}$ , or that contained in fruits, grape sugar,  $C_6H_{12}O_6$ , or from the easily transformed starch.

TABLE XII.<sup>1</sup>—QUANTITY OF SUGAR IN 100 PARTS IN

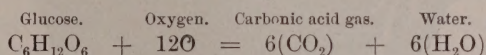
|                               |       |                            |      |
|-------------------------------|-------|----------------------------|------|
| Cherries . . . . .            | 18.12 | Goats' milk . . . . .      | 5.80 |
| Juice of sugar cane . . . . . | 18.00 | Cows' milk . . . . .       | 5.20 |
| Apricots . . . . .            | 16.48 | Indian corn-meal . . . . . | 3.71 |
| Peaches . . . . .             | 11.61 | Rye flour . . . . .        | 3.46 |
| Pears . . . . .               | 11.52 | Barley meal . . . . .      | 3.04 |
| Sweet potatoes . . . . .      | 10.20 | Wheat flour . . . . .      | 2.33 |
| Beet roots . . . . .          | 8.00  | Oatmeal . . . . .          | 2.19 |
| Parsnips . . . . .            | 4.50  | Beef's liver . . . . .     | 1.79 |

The vegetable sugars only differ from the animal varieties in the proportion of water they contain, and when we come to study digestion and absorption we shall see that the vegetable sugars are all metamorphosed into the animal kind before they are taken up by the system. While the two classes of sugars have many affinities, yet they differ in the effects produced upon them by alkalies and acids. Cane sugar, when boiled with an acid, is converted into the animal variety, the addition of alkalies having no effect. On the other hand, the acids have no effect upon the animal sugars, whereas melacic acid results from boiling with an alkali. Under certain circumstances, sugar ( $C_6H_{12}O_6$ ) becomes lactic acid,  $2(C_3H_6O_3)$ ; the significance of this chemical change we shall see presently. A convenient test for sugar is that known as Trommer's test. The suspected liquid is placed in a test-tube, to this are added one or two drops of sulphate of copper; then the mixture is made distinctly alkaline by the addition of a solution of caustic potash. The mixture will become blue, particularly if sugar is present. Now heat the test-tube till just before boiling point, when, if sugar is present, a reddish precipitate will appear just in the upper part of the tube, and will gradually be seen in the whole liquid. The reaction is due to the cupric oxide being reduced to the condition of a cuprous oxide by the oxidation of

<sup>1</sup> From Dalton, op. cit., p. 54. Payen, op. cit.



the sugar. The solution to be examined should be clear. This can be accomplished by boiling the suspected tissue, finely divided, with water and sulphate of soda and filtering. The organic and coloring matters will be retained, and a clear extract will pass through, the soda not interfering with the test. Milk, liver, and grape sugar and glucose respond to Trommer's test. Cane, maple, and beet sugar, however, must be boiled with very weak sulphuric acid to convert them into glucose before the test will be applicable. There are substances in the healthy urine which interfere with the reaction in the reduction of the copper, though sugar be added in considerable quantity. Of course, this does not apply to diabetic urine. Albuminose, which, as we shall see hereafter, is produced during gastric digestion, interferes also with Trommer's test, as noted by Longet,<sup>1</sup> though Dalton<sup>2</sup> pointed out first the fact of the products of stomach digestion having this curious effect. With the above qualifications, Trommer's test is very reliable and easily applied. Other tests, such as those of Moore, Barreswil's, Mau-merie, Bottger's, Fehling's, the fermentation test, and that of torulæ, etc., are also used. Notwithstanding the amount of sugar introduced into the economy in the food and produced independently in the system, none appears in the excretions in health; the presence of sugar in the urine, for example, being a sign of the disease diabetes. With the exception of the places indicated, sugar is not found in the system, it being destroyed almost as rapidly as produced, being burnt up and oxidized, and passing out of the economy principally through the lungs, transformed into carbonic acid gas and water thus:



Through its combustion it is one great source of heat, and hence its importance to man as a source of fuel and force. Its relations in this respect will be again pointed out when the subjects of food and animal heat are considered. At all periods of life sugar is a most important principle. In the fœtus, even at an early period of intrauterine life, the fluids contain it, and in a greater proportion than after birth.

FAT.—Fat is an almost universal constituent of the body; it is absent, however, in the bones, teeth, the eyelids, and scrotum, elastic and unelastic fibrous tissue. It is always present, even in extreme cases of emaciation, in the orbit, and around the kidneys. The amount, however, varies very considerably in the different tissues, as may be seen from Table XIII.

TABLE XIII.<sup>3</sup>—QUANTITY OF FAT IN 100 PARTS OF TISSUE.

|                            |       |                           |      |
|----------------------------|-------|---------------------------|------|
| Sweat . . . . .            | 0.001 | Liver . . . . .           | 2.4  |
| Saliva . . . . .           | 0.02  | Muscles . . . . .         | 3.3  |
| Lymph . . . . .            | 0.05  | Hair . . . . .            | 4.2  |
| Chyle . . . . .            | 0.2   | Milk . . . . .            | 4.3  |
| Mucus . . . . .            | 0.3   | Cortex of brain . . . . . | 8.0  |
| Blood . . . . .            | 0.4   | Medulla . . . . .         | 20.0 |
| Cartilage . . . . .        | 1.3   | Nerves . . . . .          | 22.1 |
| Bone . . . . .             | 1.4   | Spinal cord . . . . .     | 23.6 |
| Crystalline lens . . . . . | 2.0   | Adipose tissue . . . . .  | 82.7 |

<sup>1</sup> Gazette Heb., 1855.<sup>2</sup> Amer. Journ. Med. Sci., 1854.<sup>3</sup> Carpenter: Physiology, 1881, p. 88.

Thus, while in the sweat, lymph, saliva, etc., there is a mere trace of fat, more than twenty per cent. is found in the nervous system, and over eighty in adipose tissue. The whole amount of fat, according to Burdach,<sup>1</sup> in the body of a man weighing 176 pounds was 8.8 pounds, or 5.2 pounds of fat to every 100 of body.

Fat exists in the adipose tissue, for example, in the form of vesicles which are transparent and contain the oily matters, and in certain tissues, like the liver, cartilages, etc., an excess of the production of fat in liver cells constitutes fatty liver globules. Chemically speaking, fat consists of a mixture of the principles known to chemists as stearin, palmitin, margarin,<sup>2</sup> and olein. The first two are solid at the temperature of the body, but are held in solution by the olein. They crystallize (Fig. 12) in needle-like forms, assuming a beautiful radiatory

FIG. 12.



Stearin crystallized from a warm solution in olein. (DALTON.)

or arborescent appearance, where fluid, fatty, oily substances under the microscope have the appearance of round globules, bright in the centre, and dark at the edges. With the exception of the phosphorized fat of nervous tissues, fat does not exist combined with the other proximate principles, like we found was the case with the inorganic principles and the sugars; there is no such molecular union of fat with any principle. There is no difficulty, therefore, in extracting it from the system in a state of purity. Pressure is often the only process needed, the oil being squeezed out of the interstices of the tissues of the organ containing it. The general composition of fat may be illustrated by that of stearin,  $C_{57}H_{110}O_6$ , and it will be observed that while fat, like the carbohydrates, consists of carbon, hydrogen, and oxygen, the last two elements do not exist in fat in the proportions to form water.

<sup>1</sup> *Traité de Physiologie*, tome viii. p. 80. Paris, 1857.

<sup>2</sup> Margarin probably consists of a mixture of stearin and palmitin.

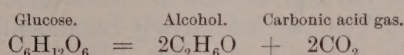


TABLE XIV.<sup>1</sup>—QUANTITY OF FAT IN 100 PARTS OF FOOD.

|                         |       |                      |      |
|-------------------------|-------|----------------------|------|
| Chocolate nut . . . . . | 49.00 | Salmon . . . . .     | 4.85 |
| Sweet almonds . . . . . | 24.28 | Cows' milk . . . . . | 3.70 |
| Indian corn . . . . .   | 8.80  | Beans . . . . .      | 2.50 |
| Fowls' eggs . . . . .   | 7.00  | Wheat . . . . .      | 2.10 |
| Mackerel . . . . .      | 6.76  | Peas . . . . .       | 2.10 |
| Calf's liver . . . . .  | 5.58  | Oysters . . . . .    | 1.51 |
| Beef's flesh . . . . .  | 5.19  | Potatoes . . . . .   | 0.11 |

The fat of the body is, to a great extent no doubt, derived from the fat of the food, somewhat modified, however, after being introduced into the system, since the fat of the body neither in man nor animals is identical with that of their food. In most cases, however, more fat is produced in the system than can be accounted for by the fat derived from the food. The experiments of Persoz,<sup>2</sup> Boussingault,<sup>3</sup> Thomson,<sup>4</sup> Lawes<sup>5</sup> and Gilbert, and others, upon geese, ducks, pigs, cows, etc., with reference to this point are conclusive.

In the case of a cow, for example, under the observation of Voit, and to be referred to again in a moment, it was observed that of the 2024 grammes of fat in the milk, only 1658 could have been derived from the fat of the feed. Now, from such facts as the starch of plants becoming oil, and of sugar being readily transformed into alcohol and other fats during fermentation, as shown by the formula



of carbohydrate principles constituting a part of a fattening food, of the negroes and cattle getting fat during the time that the cane is being collected and the sugar extracted, etc., one would be naturally led to suppose, as indeed held by Liebig, that the fat produced in the system over and above that absorbed from the food, was derived from its carbohydrate principles. On the other hand, it is a matter of every day observation that animals are fattened best on a feed consisting of albuminous as well as of carbohydrate principles apart from the fatty matters contained in it; and while there is no difficulty in understanding how, through the abstraction of oxygen, as just shown, a fat, like alcohol, may be derived from a carbohydrate, it does not follow that fat is actually so produced in the system. On the contrary, as shown by Pettenkoffer<sup>6</sup> and Voit, so far from the fat produced being proportional to the carbohydrate principles, which ought to be the case on such a supposition, the fat deposited is proportional to the amount of albumen destroyed. Thus, as will be seen from the following experiments made upon dogs fed with starch:

## EXPERIMENT OF FEEDING A DOG UPON STARCH.

|        | Starch of food. | Meat of body destroyed. | Fat deposited. | Carbonic acid produced. |
|--------|-----------------|-------------------------|----------------|-------------------------|
| No. 1. | 379 grammes     | 211                     | 24             | 546                     |
| " 2.   | 608 "           | 193                     | 22             | 799                     |

<sup>1</sup> Dalton, op. cit., p. 62. Payen, op. cit.<sup>2</sup> Annales de Chimie et Physique (3), t. xiv, p. 408, 1845.<sup>4</sup> Ann. de Chimie u. Phar., Band lxi. S. 228, 1847.<sup>5</sup> Report of the British Association for the Advance of Science, 1852.<sup>6</sup> Zeits. für Biologie, Band ix. S. 435, 1873. Hermann: Physiologie, Sechster Band, 1881, S. 252.<sup>3</sup> Ibid., p. 419, 1845.

that while the amount of fat deposited differed but little, the amount of starch taken as food was much greater in the one case than the other. This is as might have been expected, since the starch, after being transformed within the system into sugar, is then ultimately oxidized, and, as we shall see, constituting an important source of heat, cannot, therefore, be a source of fat. The meat destroyed, it may be mentioned in the above experiments, was that of the body, since none was given as food. On the other hand, in the three following experiments :

## EXPERIMENT OF FEEDING A DOG UPON STARCH AND MEAT.

|        | Starch of food. |           | Meat destroyed. | Fat deposited. |
|--------|-----------------|-----------|-----------------|----------------|
| No. 1. | 379 grammes     | . . . . . | 211 of body.    | 24             |
| " 2.   | 379 "           | . . . . . | 608 } of        | 55             |
| " 3.   | 379 "           | . . . . . | 1469 } food.    | 112            |

also made upon dogs fed with starch, and in the second and third experiments with meat also, it will be observed that while the amount of starch remained the same, that of the meat consumed differed considerably, nearly seven times more meat being destroyed in the third example than in the first, and nearly five times as much fat deposited. Not only, however, has it been shown that the meat or its contained albumen, when broken up, accounts for the production of fat in a carnivorous animal, as the dog, but also in a herbivorous one, like the cow. Thus, according to Voit,<sup>2</sup> as has already been mentioned, of the 2024 grammes of fat in the milk of a cow, 1658.40 grammes are clearly derived from the fat of the feed, 1851 grammes are developed out of the breaking up of 3602 grammes of albumen, which, together with that of the feed, more than accounts for that found in the milk, as shown in detail from the following experiments :

## PRODUCTION OF FAT IN MILK OF COW.

|                                |           |                      |   |   |
|--------------------------------|-----------|----------------------|---|---|
| In feed                        | . . . . . | 2757.74 grammes fat. |   |   |
| In feces                       | . . . . . | 1099.33              | " | " |
| Absorbed                       | . . . . . | 1658.40              | " | " |
| Out of 3602 grammes of albumen | . . . . . | 1851.00              | " | " |
| Available                      | . . . . . | 3509.00              | " | " |
| In milk                        | . . . . . | 2024.00              | " | " |
|                                |           | 1485.00              | " | " |

When the chemical composition of albumen is considered, consisting, as we shall see as it does, of CHONS, it becomes perfectly apparent how, in being decomposed in the system, it can split into two substances, a non-nitrogenous one, consisting of CHOS, and a nitrogenous one,  $\text{CON}_2\text{H}_4$ , urea, the former, excluding the sulphur, being retained in the system as fat, the latter being eliminated, as we shall see, in the urine. Suppose, for example, that 540 grains (about 34 grammes) of urea have been excreted by a man in the urine, involving a destruction of about three times as much albumen ; while all of the

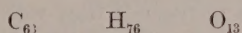
<sup>1</sup> Hermann, op. cit., S. 255.



nitrogen of the albumen destroyed passes practically out of the body as urea, only 108 grains of the 864 grains of the carbon of the albumen leave the body in that form; 756 grains of carbon are, therefore, retained in the body, available for the production of fat, as may be seen from the following formula:

|                 | C     | H     | N     | O     |
|-----------------|-------|-------|-------|-------|
| Albumen . . . . | 864   | 112   | 252   | 352   |
| Urea . . . .    | 108   | 36    | 252   | 144   |
|                 | <hr/> | <hr/> | <hr/> | <hr/> |
| Fat . . . .     | 756   | 76    | ...   | 208   |

or dividing by atomic weights.



It is not to be supposed, however, that all of the 756 grains of the carbon are converted into fat, since probably two-thirds are exhaled from the body in the form of carbonic acid. The above theoretical consideration is fully borne out by the experiments of Pettenkofer and Voit<sup>1</sup> made upon dogs fed with meat. In one instance, for example, when a dog had eaten 2000 grammes of meat (about 400 of albumen) 43 grammes of carbon were retained in the system in the form of 58 grammes of fat, corresponding to 12 per cent. of the albumen destroyed. The details of the experiment are as follows:

#### EXPERIMENT OF FATTENING A DOG ON MEAT.

|                              | N     | C     |
|------------------------------|-------|-------|
| 2000 grammes of meat . . . . | 68.0  | 250.4 |
| Urine . . . .                | 66.5  | 39.9  |
| Feces . . . .                | 1.4   | 9.2   |
| Respiration . . . .          | 0.0   | 158.3 |
|                              | <hr/> | <hr/> |
|                              | 67.9  | 207.4 |

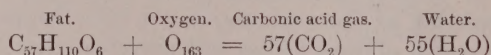
43 C retained.

Apart from the experimental evidence such as that just offered, there are a number of general facts which go to show that in many cases albumen becomes fat, as, for example, in the fatty degeneration of the tissues, the conversion of dead bodies into adipocere, the development of fat out of peptones during fermentation; that milk, after standing, contains albumen and less fat; that in phosphorous poisoning, as the fat increases the albumen diminishes, etc. Many more instances might be mentioned, but enough has been said to leave no reasonable doubt that fat, to a certain extent at least, is developed out of albumen. The only question that still remains undecided is as to what extent albumen becomes fat. In many instances, according to Voit,<sup>2</sup> even if as little as ten per cent. of fat (fifty per cent. being the maximum) is developed out of albumen, the amount so developed, together with the fat present in the food, is more than enough to cover the fat produced

<sup>1</sup> Zeit. für Biologie., v. S. 106, 1869; vi. S. 371, 1870; vii. S. 489, 1871.

<sup>2</sup> Hermann: Physiologie, Sechster Band, S. 255.

by the animal. On the other hand, there is no positive evidence whatever that carbohydrate principles are transformed within the body into fat. As a matter of fact, they cannot be drawn upon for that purpose to any extent, leaving the body as carbonic acid and water after having been oxidized in the system. General considerations and experiments showing then that the fat deposited in the body over and above that absorbed from the food is derived from albumen, it may be asked of what use are the carbohydrate principles always present in fattening diet; in what way do they contribute toward the production of fat? Regarding these principles as a source of heat to the economy, their rôle as a part of fattening diet becomes perfectly clear, since in being burned they save the fat otherwise derived and which would be drawn upon for the same purpose if they were absent. Hence, the fact of a dog fed on sugar and meat, excreting less urea and getting fatter than when fed on meat alone, of the negroes, etc., already referred to, getting fat during the extraction of the sugar from the cane; of dogs fed on meat and rubol,<sup>1</sup> palm oil,<sup>2</sup> or stearin, getting fat, and without a trace of these substances being found in the excreta, the sugar or oil given with the food in these instances saving the fat otherwise produced from the albumen from being burned. The carbohydrate principles evidently then play in the production of fat this secondary rôle of saving the fat, otherwise produced, from being consumed, and only in the event of it being shown that the fat deposited cannot be accounted for by the destruction of the albumen being overestimated, can these principles be regarded as a source directly of fat, of which at present, I repeat, there is no evidence. If the view of the origin of fat, just referred to, essentially that of Voit,<sup>3</sup> be accepted, it becomes intelligible why individuals become fat whatever they eat, and that if the fat of the body is to be reduced, all kinds of food must be diminished, as little eaten as possible, to cut off the supply, and plenty of active exercise taken to quicken the circulation and respiration, and in that way burn off that already deposited. Fat is never discharged from the body in health except in the butter of milk, but is destroyed, burnt, passing away as carbonic acid gas and water; and, therefore, like sugar, being a source of heat and force:



Fat is useful also as serving to support the organs, like the eye and kidney. It fills up the spaces between vessels, bones, and muscles, rounding off the trunk and extremities into the graceful curves of the human form.

It prevents the loss of heat through its bad conductive power. This function of fat is well shown in the cetacea, of which the whale, dolphin, and porpoise are examples. In these animals, just under the skin, there is an immense amount of blubber or fat. If it were not for this layer of fat these marine animals would lose a great quantity of heat.

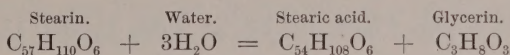
<sup>1</sup> Radziejewsky: Virchow's Archiv, xliii. S. 268.

<sup>2</sup> Subbotin Zeits. für Biologie, Band vi. S. 73, 1870.

<sup>3</sup> Hermann: Physiologie, Sechster Band, S. 235.



It is well known that when fat is boiled with an alkali and water, part of the water is appropriated and the fat breaks up into glycerin and oleic, palmitic, or stearic acid, according to the kind of fat used, the acid further uniting with the alkali to form soap. This process is called saponification, but the term also includes the breaking up, simply, of fat, in the presence of water, into glycerin and an acid, as seen in the following formula :



This can be accomplished by passing the vapor of water through fat heated to  $572^{\circ}$  F. In this way, sodium oleate and palmitate and oleic and palmitic acids are formed. I mention these principles, as they have been found in small quantities in the blood, bile, and lymph. The odor in the axilla and feet is probably due to the combination of fatty acids with alkali. The oleates and margarates may serve to hold in solution the small amounts of fat and fatty acids found in the blood. Some of the fat introduced in the economy probably disappears through this process of saponification. As regards the remaining proximate principles of the second class, lactic acid, pneumatic acid, and sodium pneumatate, little need be said. Lactic acid is developed in the economy through the "acid fermentation" of sugar, especially that of milk; as seen, for example, in the souring of milk. It is found in the muscles and often in the gastric juice. Pneumatic acid is restricted to the lungs. Pneumatate of soda is formed through the decomposition of the carbonates in the blood as the latter pass through the lungs.

## CHAPTER III.

### PROXIMATE PRINCIPLES OF THE THIRD CLASS.

THIS class includes such substances as albumen, fibrin, casein, pepsin, globulin, ostein, etc. They agree with the principles of the second class, in being of organic origin—that is, elaborated by plants and animals, organized bodies. The water, carbonic acid, and salts found in the mineral inorganic world, constituting the food of plants, with some exceptions, like the fungi, are converted by the plant through the agency of the sun's light and heat into such principles as starch, sugar, vegetable albumen, fibrin, and casein, etc. The plants in time serve as food for herbivorous animals, which are eaten by the carnivorous ones, while, as we shall soon see, all three, plants, herbivora, and carnivora, together with the inorganic principles, enter into the food of man.

It will be seen, therefore, that, so far as the organic principles are concerned in nature, the plant is indispensable as preparing the food for the animal; the former living on carbonic acid, salts, etc., which would be starvation to the latter.

While the organic principles are usually developed in the order indicated, it must be mentioned, however, that chemists have succeeded in artificially preparing some of the principles of the third class, as well as those of the second, from the direct combination of the inorganic elements in their laboratory by purely physico-chemical processes, without invoking in any way either plant or animal agency.

Just as no sharp line of demarcation can now be drawn between plants and animals, so the distinction between the organic and inorganic worlds is daily becoming fainter. Indeed, no one can say positively where the one ends and the other begins.

The proximate principles of the third class, with the exception of lecithin, cerebrin, leucin, tyrosin, to be described hereafter, differ from those of the first and second in not being crystallizable. They may coagulate, but they never assume regular crystalline form.

It is usually assumed in works on physiology that such substances as albumen, fibrin, etc., have not a definite chemical composition and therefore differ in this respect from water, salt, sugar, etc. Chemistry teaches that a definite quantity by weight of oxygen and hydrogen unite to form a definite quantity of water; that a certain quantity of sodium chloride consists of just so much sodium and chlorine; that carbon, hydrogen, and oxygen combine in certain proportions to form a definite quantity of sugar. If, however, any of the elements entering into the composition of these substances be either increased or decreased, the substance will cease to exist as such: *à priori* then it is highly improb-



able that albumen, for example, consisting of  $C_{72}H_{112}N_{18}O_{23}S$ , should be an exception to this law of definite combining proportions. It seems to me more likely that albumen differs in its composition in individuals and is constantly changing even in the same person, and that these albumens, while resembling the one whose formula has just been given, if carefully analyzed would be found to consist of different amounts of carbon, hydrogen, oxygen, nitrogen, and sulphur, with different properties, than to suppose that the composition of a substance like albumen can be altered without affecting its properties, and that it has no definite chemical composition. That such is the case seems confirmed by the fact of chemists having described at least sixteen kinds of albumen.

The truth seems to be that any one of these albumens, with a little more or a little less of this or that element of composition, is not so changed as to render it unfit for playing the ordinary rôle of albumen in the economy. In other words, that these albumens, though slightly differing chemically, are readily converted into one another, the function of albumen in the system being performed by any of them.

This, however, is quite a different statement from that usually made, that these principles are of indefinite chemical composition.

The proximate principles of the third class, however, are distinguished in a marked degree from those of the first and second in containing nitrogen. This element seems indispensable to the composition of a body exhibiting life. As is well known, those substances which are very changeable, decomposing suddenly, like nitrogen iodide, nitrogen chloride, nitroglycerin, fulminating salts, gunpowder, etc., owe their peculiar properties to the nitrogen they contain.

As we proceed in our studies, we shall see that the essence of life is in change. To make use of a homely simile, nitrogen seems to play the same part in the living body as that by a restless, excitable spirit in the living community; ever ready himself to be affected by slight changes and to influence in the same way those around him.

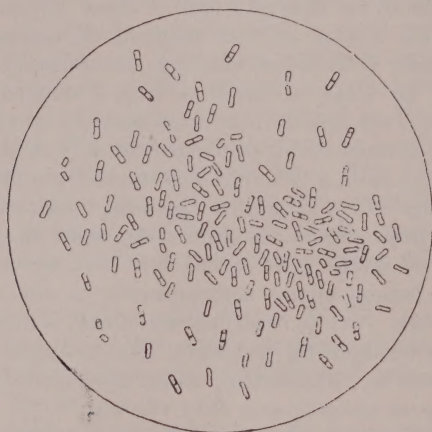
Thus an important feature of the nitrogenized proximate principles is the readiness with which they induce such changes as fermentation and putrefaction—the latter being brought about by the growth and multiplication of a minute protist, the *Bacterium termo* (Fig. 13), just as sugar is decomposed into alcohol and carbonic acid through the influence of the yeast cell. Like the latter, the bacterium cells in inducing putrefaction neither give up nor take away any chemical elements, acting by their presence alone in a way which <sup>it</sup> must be admitted, is not as yet understood. The effect of the bacterium cells in inducing putrefaction in this manner, like that of the *saccharomyces* or yeast cell (Fig. 14) in producing fermentation, is usually said to be due to catalysis. The word catalysis meaning literally to dissolve, break up, while frequently made use of in speaking of those actions in the economy which are of this character, is, however, only a word, not an explanation—in fact, merely a convenient way of expressing our ignorance of the phenomena to be explained.

The susceptibility of these organic principles to change, in and out of the body, is not only due to the nitrogen they contain, but to the great number of atoms entering into their composition.

It is more natural that albumen, for example, consisting of 225 atoms, should break up into its constituent parts on the slightest change taking place in the surrounding conditions, than sodium chloride or water, composed of two or three atoms respectively. It is easier for two or three persons to get along together than 225, especially when among the latter there are 22 (the nitrogenous atoms) most unstable ones.

Another property of these principles is their hygrometricity—that is, their capacity for taking up their water of composition by contact after it has been driven off by heat, when the principles are said to have been desiccated.

FIG. 13.

Cells of *Bacterium termo*; from a putrefying infusion. (DALTON.)

The organic principles of this class are always combined with the inorganic ones, the union being most intimate, so much so that as the first are used up and become effete, and are cast out of the body, the inorganic principles go with them. Like the principles of the second class, those of the third class are destroyed in the system, never appearing in the excretions in health (with the exception of casein of milk, mucus, epithelium, and epidermis). Being transformed into carbonic acid, water, urea, etc., through a process of splitting, with subsequent oxidation, they are also a source of heat to the economy like the principles of the second class. The different principles of this class, and some of the situations in which they are found in the human body, may be seen in

TABLE XV.'—QUANTITY OF ALBUMEN.

| Substance.                     | Parts per 1000. | Substance.                        | Parts per 1000. |
|--------------------------------|-----------------|-----------------------------------|-----------------|
| Cerebro-spinal fluid . . . . . | 0.9             | Chyle . . . . .                   | 40.9            |
| Aqueous humor . . . . .        | 1.4             | Spinal cord . . . . .             | 74.9            |
| Liquor amnii . . . . .         | 7.0             | Brain . . . . .                   | 86.3            |
| Intestinal juice . . . . .     | 9.5             | Liver . . . . .                   | 117.4           |
| Pericardial fluid . . . . .    | 23.6            | Muscle . . . . .                  | 161.8           |
| Lymph . . . . .                | 24.6            | Blood . . . . .                   | 195.6           |
| Pancreatic juice . . . . .     | 33.3            | Middle coat of arteries . . . . . | 273.3           |
| Synovia . . . . .              | 39.1            | Crystalline lens . . . . .        | 383.0           |
| Milk . . . . .                 | 39.4            |                                   |                 |

<sup>1</sup> Carpenter, op. cit., p. 60



Their relative amount, as may be seen, varies greatly; thus in a thousand parts of cerebro-spinal fluid there are only traces of albuminous compounds, over 30 parts in the same amount of chyle, and nearly 200 in blood. In the brain, over 80 parts to the thousand, over 160 in muscle, and nearly 400 in the crystalline lens, in round numbers. The principles of this class all agree in their general aspects; a few words will suffice for their individual peculiarities.

ALBUMEN.—Albumen, which the white of egg closely resembles, is the type of the other principles of this class, and out of which they are all elaborated. It is found in all parts of the system, at all periods of life, in greatest abundance in the blood, is present in the lymph, chyle, serous secretions, milk, intermuscular fluid. Albumen can be obtained from the system, in which it exists in the fluid condition, by coagulation. This can be readily done by heating, or adding alcohol to the liquid containing the albumen, and filtering. Mineral acids, and some of the metallic salts, have the same effect. *(the source)*

The ordinary method of testing for albumen consists in heating the suspected liquid—urine, for example—in a test-tube, when, if albumen be present, an opacity makes its appearance in the upper part of the tube first, which afterward extends downward, an insoluble precipitate is formed, which often becomes solidified.

If it be thought that the opacity be due to an excess of earthy phosphates, add hydrochloric acid, which has no effect on coagulated albumen, but which will dissolve the phosphates. On the other hand, caustic potash will dissolve coagulated albumen in urine, but has no effect on the phosphates. In adding nitric acid to urine it may be mentioned that the cloudiness is often due to urates; this will disappear in an excess of nitric acid, which, however, will not take place if the cloudiness be due to coagulated albumen, and it should be added that, in making use of the heat test, etc., the liquid to be tested, if alkaline, will not respond, even though it should contain albumen; under such circumstances it is necessary to add a few drops of acetic acid.

The albumen of the blood is derived from the albuminous substances of the food, the latter, as we shall see, being transformed during digestion into albuminose, an albumen intermediate between food albumen and blood albumen.

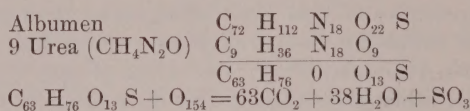
Blood albumen, the great nutritive element of the blood, is carried by the latter medium to all parts of the system. In this way the tissues are supplied with fresh nitrogenized material, replacing that which becomes effete.

The actual process by which the albumen of the blood is transformed into the albuminous principles of the tissues during growth, or in adult life, has not yet been made out. There is no reason to doubt, however, that, like all other so-called vital phenomena, it is a physico-chemical one.

Albumen, after splitting up into simpler compounds, and subsequent oxidation of the latter, leaves the body as urea, carbonic acid gas, and water. It is, therefore, a source of heat and force to the economy as well as a tissue-maker, and this is true of the albuminoids generally.

Adopting at least provisionally, the formula for albumen already

given, and deducting its nitrogen as representing so much urea, it will be at once seen that the remainder of the albumen, through oxidation, will finally be transformed into carbonic acid, water, and sulphuric acid, even if it be supposed that part of the albumen is retained temporarily as fat, as follows:



It is obvious also, that if the fat developed out of the albumen be finally burned, nevertheless the combustion of albumen will be far less perfect than that of sugar or fat, since thirty-two per cent. of the albumen passes, unburned, as urea, out of the body. Albumen, as a source of heat to the economy is, therefore, an expensive fuel, so to speak, as compared with sugar or fat, which are as perfectly burned within the body as out of it; apart, also, from the fact of less heat being developed through the burning of albumen than of equal parts of fat or sugar.

**ALBUMINOSE.**—Albuminose, or the modified food albumen, is found in the stomach and small intestine during digestion, and immediately afterward in the blood in small quantities. It differs from the albumen of the blood in not being coagulable by heat, and imperfectly by nitric acid, and from the albumen of the food in being endosmotic—that is, capable of passing through membranes, and so of being absorbed and getting into the circulation.

White of egg, though not identical with albumen, but closely resembling it, was shown by Bernard<sup>1</sup> to be rejected by the kidneys when injected into the veins, due probably to its not being endosmotic.<sup>2</sup> When the white of egg has been digested, however, and converted into albuminose, it is then readily absorbed.

Albuminose does not remain long as such in the blood, being rapidly transformed into blood albumen.

**FIBRIN.**—It is questionable whether the substance commonly called fibrin exists as such, as a proximate principle in the system. When the blood coagulates, and the red corpuscles are removed from the clot, there remains a whitish, stringy, fibrous substance called fibrin, and which is supposed by some chemists to exist as such in the blood in a fluid condition; by others, to be only an albumen, modified through changed conditions; another view favored by many, is that fibrin is due to the union through a ferment of two principles—fibrinogen, found in the liquor sanguinis, and paraglobulin, found in the blood corpuscles.

There is much to be said in favor of all these views, but, as we shall see later, as yet the origin of fibrin cannot be said to have been positively determined.

This substance is found in the lymph and chyle as well as in the blood, but in less quantity. It is composed ultimately of the same elements as albumen, and must, therefore, be derived, remotely, from the nitrogenized principles of the food.

<sup>1</sup> Bernard: *Liquides de l'Organisme*, tome i. p. 467. Paris, 1859.

<sup>2</sup> Mialhe: *Chimie Appliquée à la physiologie*, p. 125. Paris, 1856.



Whatever its condition may be in the blood, in the system fibrin is destroyed; thus it is not found, for example, in the renal or hepatic veins, the liver and kidney transforming it in a way not yet understood.

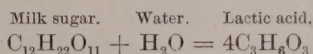
Fibrin is interesting to the pathologist, as constituting the false membrane of croup, and as supplying the material for the spontaneous arrest of hemorrhage in small vessels which have been opened from any cause.

**CASEIN.**—This principle is found only in the milk, being derived from the albumen by the action of the mammary glands, and is therefore present in the system only during lactation.

It is very important, however, as constituting the principal nitrogenized food for the infant, being readily converted in the child into albuminose, which is carried into its blood and is then transformed into blood albumen.

It is one of the few principles of this class which are discharged from the body in health. It differs from albumen in not being coagulated by heat, but by the weak vegetable acids.

The coagulation of casein occurs when sugar of milk is converted into lactic acid by hydration, the milk becoming then sour, the reaction being as follows:



Casein is kept in a fluid condition in milk through sodium carbonate.

**MUCOSIN, PANCREATIN, PEPSIN.**—Mucosin is found in the secretions of mucous membranes, differing slightly in composition according to the situation from which it is obtained. It is very like albumen; indeed, the white of the egg is generally taken as the type of albumen, though it is really mucosin, being secreted by the mucous membrane of the oviduct of the hen. White of egg differs from ordinary mucosin, however, in usually containing sulphur. Mucosin is one of the few principles of the third class discharged in health.

Pancreatin is the active principle of the pancreatic juice. It differs from albumen in being coagulated by magnesium sulphate. Its properties with those of pepsin, the nitrogenized element of the gastric juice, will be considered when the subject of digestion is taken up.

**OSTEIN AND CARTILAGIN.**—This principle, which is solid, is found only in bones, in combination with the earthy salts. When bone is treated with dilute hydrochloric acid the mineral salts are dissolved out and almost pure ostein remains.

When bones are boiled they are converted into gelatin. This, however, is not a proximate principle, as it does not exist as such in the system.

Cartilagin is to cartilage what ostein is to bone. When cartilagin is boiled it becomes chondrin. This goes to show that the development of bone from cartilage is more than the addition of lime salts; the organic principle cartilagin being probably metamorphosed at the same time into ostein.

**GLOBULIN, CRYSTALLIN, MUSCULIN.**—Globulin and crystallin exist in a semisolid state in the blood corpuscles, and crystalline lens of the

eye respectively. Musculin is found also semisolid in muscles, combined with inorganic principles. It is the most important nitrogenized element of the food, and through its metamorphosis into albumen in the system supplies, to a great extent, the economy with that important principle.

**ELASTICIN AND KERATIN.**—Elasticin is found in the yellow elastic tissue and the membrane which envelops the muscular fibres. Keratin is present in the nails and hair.

**HÆMATIN, MELANIN, BILIVERDIN, UROSACIN.**—Hæmatin gives the blood its red color, and is found in the corpuscles combined with globulin. One of its most important constituents is iron.

When hæmatin is deficient in the system as seen in anæmia, the exhibition of iron will always reproduce it.

To demonstrate iron in hæmatin, add one drop of nitric acid to blood in a watch glass, and evaporate over a lamp. The iron is converted into a peroxide (the acid giving up oxygen), to this add the potassium sulphocyanide, when the characteristic red color will appear, due to the formation of the ferric sulphocyanide.

Melanin is the organic principle of pigment found in the choroid and iris of the eye, hair, and epidermis. It is probably developed through the transformation of hæmatin.

Biliverdin, the coloring matter of the bile, and urosacin, the modified pigment of the urine, will be again referred to under the subjects of the liver and kidneys.

To avoid repetition, as well as for convenience, the remaining proximate principles entering into the composition of the tissues and secretions of the body, and not mentioned in the general introductory just given, will be considered as the latter are successively treated of.

While there is no doubt that the urea, carbonic acid, and water of the excreta are derived from albuminous principles, there is still a difference of opinion as to whether the albumen whose breaking up and oxidation gives rise to urea, etc., is that of the tissues or that of the food, or of both, and, if the latter, how much of the urea produced is to be attributed to the breaking up of the tissue-albumen and how much to food-albumen.

That the urea cannot be entirely derived from the breaking up of the albumen of the tissues, organic albumen, is shown from the amount produced in starvation being so much smaller than when nitrogenous food, circulating albumen, is taken; fifteen times as much urea being produced, according to Voit,<sup>1</sup> in the latter case as in the former. Unless this large amount of urea is derived from the food it is difficult to account for it, for although the albumen of the body exists in greater amount than that of the food, as a matter of fact in starvation but a fractional part of it is destroyed; in a dog, for example, about one per cent.

It is true that it is held by many physiologists that the albuminous principles of the food displace those of the tissues, either entirely or in part, the latter giving rise to the urea, according to the view that urea

<sup>1</sup> Hermann: Physiologie, Sechster Band, S. 302.



is derived from the tissue whether albuminous food be taken or not, all albuminous food becoming tissue before being destroyed. If such be the case, however, the whole body of a dog, for example, would be destroyed and built up again in a few days,<sup>1</sup> which is much more improbable than that its albuminous food taken during the same time should be broken up and oxidized into urea, etc. Indeed, as a matter of fact, there is no evidence to show that under any circumstances the disintegration and oxidation of the body proper, apart from that of the food absorbed, go on to anything like the extent usually assumed and embodied in the popular idea of the whole body being entirely changed in some given period.

Apart from the daily destruction and renewal of the cells of the epidermis and its appendages, hair, nails, etc., of the epithelial cells of the mucous membrane of the nose, trachea, alimentary canal, and its glandular appendages, of the blood corpuscles, there is little or no evidence of the total destruction of the cells, the constituent elements of the tissues.

Even in starvation, where the muscles and liver may diminish one-half in weight, under the microscope the same number of muscular fibres, the same number of liver cells are visible, though diminished in volume through loss of their contents, just as an *amœba*, *paramœcium* or any unicellular being may be empty or distended according as it is supplied with food; cells, the structural elements, as we have seen, being essentially distinguished from extraneous matters which they may or may not absorb.

That a disintegration and renewal of the tissues may go on is seen in the formation of bony cavities, in the production and absorption of callus, in the disappearance of the alveolar ridge of the jaw, in the reproduction of parts that are lost. Such processes, as we know, are, however, very slow, while under certain circumstances there does not appear to be any change taking place at all, depression in the crystalline lens of the eye, cicatrices, peculiar markings in the skin, etc., persisting through life.

This hypothesis of the destruction of the albuminous tissues and the derivation of urea from the latter is an illustration among many of the vast influence of Liebig's<sup>2</sup> views upon animal chemistry.

That distinguished chemist held that force was developed at the expense of the albuminous tissues, the loss being continually repaired by albuminous food; that muscular activity was the cause of the decomposition of tissue-albumen, and consequent production of urea, and that the amount of tissue-albumen destroyed is a measure of tissue change or "stoff-wechsel" as he called it—that is, the breaking up of the albuminous tissues with the production of urea and the rebuilding of the same through albuminous food. Any albumen present in the food, over and above that destroyed through muscular activity, was deposited, according to Liebig, in the body—that is, the amount of urea produced depended upon the muscular work and not upon albuminous food.

<sup>1</sup> Voit in Hermann, op. cit., S. 277.

<sup>2</sup> Die Organische Chemie, 1842. Ann. d. Chemie und Phar., xli., 1842; liii., 1845; lviii., 1846; lxx., 1849; lxxix., 1851.

The remaining carbohydrate principles, etc., of the food in being oxidized were regarded solely as sources of heat, their transformations not constituting a part of the true stoff-wechsel, that being limited to the changes in the albuminous tissues.

With the establishment, however, of the fact that the amount of urea was increased by albuminous food, independently of muscular activity, the celebrated theory of Liebig as such was no longer tenable. So deeply rooted, however, was this theory, that it was still defended, though in a somewhat modified form, by Lehmann,<sup>1</sup> Frerichs,<sup>2</sup> Bidder,<sup>3</sup> and Schmidt.

Those experimenters who first showed that urea is increased by nitrogenous food impressed with the improbability of any great quantity of the latter becoming first tissue and then urea, assumed that all of the albumen of the food over and above that destroyed in starvation (the minimum, and derived from the body) was in excess, was a *luxus*, so to speak, and was directly oxidized in the blood, like the carbohydrate principles, etc. Hence the theory so widely known as that of "*luxus consumption*."

As there is not the slightest evidence, however, that the albuminous principles of the food are directly oxidized in the blood, and, as we shall see, muscular action does not increase the amount of urea, and as the amount of albumen destroyed in starvation is no measure of that destroyed in health, the celebrated theory of "*luxus consumption*" of Bidder and Schmidt falls to the ground with that of the "*stoff-wechsel*" of Liebig, of which it is merely a modification.

As there is little or no evidence of the rapid destruction of the integral part of the tissues implied in the view of the albumen of the food becoming tissue first and afterward urea; or, it may be added, of the urea being developed synthetically out of simpler principles resulting from the destruction of the tissues, it will be assumed, for the present, at least, that by far the greatest amount of urea is produced through the splitting up of the nitrogenous food into simpler compounds, and subsequent oxidation of the latter.

By oxidation, whether of food or of tissue, it may be here as well as elsewhere mentioned, that it is not to be understood that there is a direct combination of oxygen with food or tissue, but that just as in the case of oil burning in a lamp, or of wood in a stove, there is a splitting up of these substances at a certain temperature into simpler ones, the latter of which are oxidized, so do the albumen and fat of the body split up into simpler principles, which by subsequent oxidation pass out of the system as urea, carbonic acid, and water, and just as in the imperfect combustion of oil or wood through the want of oxygen there arise various products, so the imperfect combustion of albumen, sugar, etc., gives rise to the production of fat, uric acid, diabetic sugar, etc.

That the breaking up of food or tissue in the body cannot be due to direct oxidation, as held by Lavoisier, is shown by many facts, such as that the oxidation of substances within the system does not follow the same order as without it; that animals do not breathe more oxygen

<sup>1</sup> Wagner: Handwörterbuch, 1884, ii. S. 18.

<sup>3</sup> Die Verdauungssäfte, 1852, S. 348.

<sup>2</sup> Archiv f. Anat. und Phys., 1848, S. 469.



when in an atmosphere containing a greater quantity than that existing in the ordinary air, or absorb more oxygen even though the hæmoglobin be saturated with it, that carbonic acid is exhaled by a body or part of the same in an atmosphere in which oxygen is absent. Indeed, there is no more reason to suppose that the destructive changes of food or tissue going on in the body are entirely dependent upon direct oxidation, than that the combustion of wood or coal in a stove depends entirely upon the draught. The construction of the body, like that of the stove, must exercise a great influence upon the burning of the substances placed within it.

Inasmuch as the destructive changes of food or tissue, or of both, going on in the body, and upon which the maintenance of life depends, are not due to direct oxidation, as held by Lavoisier, nor to muscular activity and oxidation, as supposed by Liebig, Bidder, Schmidt, etc., it remains for us now to offer some hypothesis which can be provisionally accepted, if for nothing more than that by its facts can be connected together, woven into something like a theory, suggestive not only of new discoveries, but to be tested by them. /ten

From time immemorial physiologists have been impressed with the similarity existing between the phenomena of fermentation, putrefaction, and those of life, and with every advance in knowledge the resemblance becomes more and more striking. Thus, as we shall see, the change of starch into glucose by the saliva, of albumen into albuminose by the gastric juice, the splitting up of fat in the presence of water into glycerin and fatty acid, etc., by the pancreatic juice, are due to the ferment-like action of the ptyalin, pepsin, pancreatin, of these secretions.

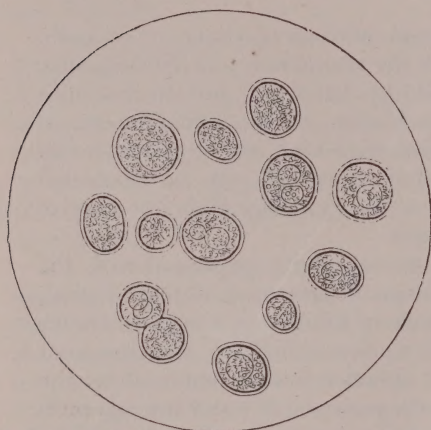
These changes are, however, but the first of a series experienced by the food in its gradual transformation into urea, carbonic acid, and water; the intermediate, subsequent stages taking place in the tissues themselves and not in the fluids bathing them. At least there is no evidence that the further breaking up and oxidation of the food modified during digestion and absorption, go on in the blood, lymph, or chyle, these fluids appearing to be rather the means of transportation of the nourishing food to the tissues where the so-called vital changes take place and of removing the effete matters to the excretory organs, by means of which they are eliminated from the body.

That the fluids of the body, such as the blood, lymph, etc., cannot be indispensable in the effecting of those changes which constitute life, apart from carrying to the tissue the material to be changed, is shown from the fact that such changes go on in an economy in the absence of blood, etc., as in the absorption of oxygen and carbonic acid by unicellular organisms, and the lower forms of animal life in which a vascular system is absent. In insects also, in which the breathing being accomplished by tracheæ, the oxygen is absorbed directly by the cells of the organs surrounding the latter, and, as we shall see later, the embryo bird, consisting, as it does, essentially of a mass of but little differentiated cells, absorbs oxygen and exhales carbonic acid in the absence of a vascular system.

Facts like those just mentioned of the fermentative changes taking place in the alimentary canal, and elsewhere, as we shall see, of the far

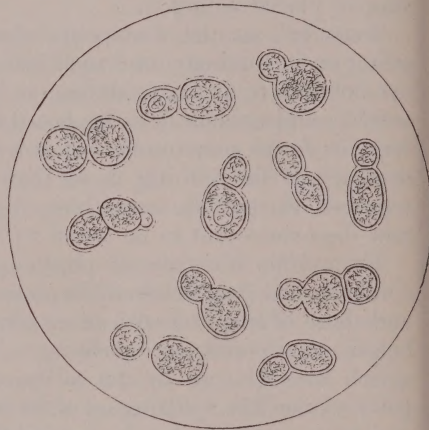
greater functional activity of the tissues, as compared with that of the fluids of the body, of the relative stability of the tissues, as contrasted with the albuminous and carbohydrate principles of the food brought to them in the fluids, point to the general conclusion that vital changes are brought about in the tissues by some kind of ferment action together with oxidation. The tissues, through virtue of the cells of which they consist, act upon the food brought to them, as the yeast cell, saccharo-

FIG. 14.



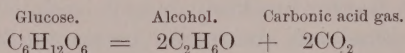
*Saccharomyces cerevisiæ*, in its quiescent condition; from deposit of beer-yeast, after fermentation. (DALTON.)

FIG. 15.



*Saccharomyces cerevisiæ* in active germination. From fermenting saccharine solution. (DALTON.)

*myces cerevisiæ* (Figs. 14, 15), acts upon sugar, breaking it up into carbonic acid gas and alcohol, as shown by the formula :



the changes undergone by the food in passing through the economy not any more necessarily involving the destruction of the tissues than the changes in the sugar induced by the yeast cells involve the destruction of the latter; though the cells of the tissue, like those of the yeast, have a certain limit to their action. It would appear, therefore, that life is rather maintained through the destruction of the food by the cells of the tissue through fermentation and oxidation than at the expense of the tissues themselves. Such at least is essentially the view so well developed by Voit,<sup>1</sup> one of the highest living authorities on the subject of nutrition, and by which many striking facts in nutrition, whether during starvation or upon a diet of one ~~one~~ or more articles of food, may be explained.

Thus while a starving man lives at the expense principally of the albumen and fat stored up in the tissues of his own body, there not being enough of these principles in the fluids to account for what is destroyed as measured by the excreta, nevertheless, the albumen and

<sup>1</sup> Physiologie der Allgemeinen Stoffwechsel und der Ernährung, Hermann, op. cit., Sechster Band.



fat of the tissues, etc., are not, as such, used as food, but are transformed into circulating or food albumen, and in this form are carried to the other tissues, and there destroyed, one part of the body being sacrificed, therefore, to nourish another. That the latter is the case, is evident from such facts as that the heart and central nervous system, for example, during starvation lose but little in weight, whereas the muscular system may be reduced over forty per cent., that the bones of the extremities do not suffer for want of lime salts, the latter being supplied from the bones of the sternum and skull, the latter becoming, in consequence, very thin, of the starving mother secreting milk in volume, etc., far exceeding that of the mammary gland itself.

As regards also the destruction of different kinds of nutritive principles, whether derived from the tissues of the body or from food, it is evident that the cells destroy more readily certain principles than others: albumen more readily than sugar, sugar more readily than fat whether derived from food or albumen. The amount of such substances destroyed or deposited will depend then on the relative amounts in which they are presented to the tissues, whether in starvation or in health.

Hence, on an excessively rich nitrogenous diet the cells exhausting themselves in destroying albumen, fat will be deposited; the same will be the case if sugar be given with albumen, the former being destroyed in preference to the fat derived from the albumen.

RÉSUMÉ.—We have seen that the proximate principles of the third class consist ultimately of carbon, hydrogen, oxygen, nitrogen, sulphur (and, in some animals, of phosphorus). That such principles as albumen, fibrin, casein, etc., should be composed of these chemical elements to the exclusion of the remaining sixty or seventy, is not meaningless. Spencer<sup>1</sup> has shown that the elements composing living bodies have mobility enough to enable them to get rid of their effete material and to change continuously and actively their intimate parts. On the other hand, through the combination of a great number of atoms, these principles, through their inertia, become relatively immobile and possess fixity enough to resist disintegration. There must be fluidity and yet solidity in a living body. These conditions are fulfilled in the fact that three of the important elements entering into the composition of albumen, fibrin, etc., are mobile gases, oxygen, hydrogen, and nitrogen, hence the readiness with which these matters change the arrangement of their parts or development, and the rapidity of those transformations of motion or function.

It can be shown on mechanical principles that as the masses of the atoms increase, their mobility decreases, hence the comparative cohesiveness of such principles as albumen, etc.

Many interesting illustrations are brought forward by Spencer in favor of the above view. Briefly, it may be said here that the chemical and physical contrasts of the carbon, hydrogen, oxygen, and nitrogen are such as, *à priori*, would be required of the elements entering into the composition of living bodies.

While admitting that the proximate principles of the third class are

<sup>1</sup> Principles of Biology.

indispensable to the production of life, it seems to me, however, that we are not justified in restricting vitality to them as is often done by physiologists. The fact is that the tissues as they exist in the living body are not composed of albuminous principles alone. What would bone be without its calcareous salts, nervous tissue without phosphorized fats, how much life would be left in a body after the water had been removed, of what use would the pepsin be in the gastric juice without the acid, the blood without its salts, iron, etc.?

It is often said that the albuminous principles impart their life to the inorganic ones. This is a mere assumption, for the former principles are always intimately associated with the latter, being taken into the body to be digested, assimilated, and excreted together.

You cannot separate the inorganic principles from the albuminous ones and leave the latter living. Deprive an animal of water and salt and it will die as surely as if deprived of albuminous food.

If there are any strictly vital principles in a living body to the exclusion of others not vital, it does not seem to me that they can, at present, at least, be isolated. A simple statement of the fact is, that life consists of a series of changes exhibited by certain inorganic and organic principles composed of chemical elements combined in a certain way under certain conditions.

The more complex the materials and their mode of combination, the more complex the resultant life.

A substance consisting of two chemical elements, one atom of each only in combination, possesses fewer properties than one consisting of numerous elements and hundreds of atoms. Water,  $H_2O$ , has fewer properties than potassium ferricyanide,  $Fe'''K_3(CN)_6$ , seen crystallized in definite mathematical form in every apothecary's window, and neither can be compared as regards their possibilities with living matter consisting of an infinite number of atoms of albuminous, carbohydrate, and inorganic principles.

Believing that the properties of water and those of potassium ferricyanide are the resultant of the properties of the chemical elements of which they consist, logically it must follow also that life results from the properties of the elements composing the substances exhibiting the life, the question in each instance being one of the redistribution of matter and force. It should be mentioned also that the connection between the elements and the properties exhibited by their union are at present as little understood in the first two cases as in the last, molecular physics not yet having given an explanation. Vital phenomena are not, therefore, more mysterious than any other kind of phenomena, and can be investigated to the same extent and in the same sense as those of gravitation, chemical affinity, etc. No more, no less. Facts obtained and laws generalized from them. The essence of phenomena, the ultimate cause of gravity, chemical affinity, vitality, or any other mode of force being unknowable.

We have seen that the proximate principles of the human body are derived directly or indirectly from the food. When we come to study the blood we shall find that it is by means of this fluid that these principles are carried to all parts of the economy. As the living body is



nourished by its blood, and as the blood is being continually renewed by the food, it is natural that all three, body, blood, and food, should contain essentially the same principles. We shall soon see that this is the case. As the nutritive principles exist, however, in the food in a condition different from that found in the blood, they are first subjected to certain processes in the alimentary canal that render them susceptible of absorption by this fluid and the lymph; whence carried to the tissues they are further elaborated, assimilated, or decomposed by the cells of the same, supplying the latter with material for growth and development or the production of force.

The life of the body, as already stated, being the total life of the cells composing it, it is in the cells or their modifications that the elaboration, combination, and decomposing of the chemical principles take place, the total resultant of which constitutes life. To the first of such vital processes, digestion, let us now turn, commencing with the subject of food.

## CHAPTER IV.

### FOOD.

VITAL, like all other work, implies waste. Our thoughts, our words, our gestures are all accomplished at the expense of the food and tissues of our bodies. Portions of our tissues, and the food appropriated by them, are being slowly but constantly consumed, being transformed into substances which will ultimately become carbonic acid, water, and urea.

Life depends upon this continual and incessant waste and change of food and tissue. It is literally true that "in the midst of life we are in death." Every mental and muscular effort is accompanied with the destruction of so much food, brain, and muscular substance, and the loss of heat. The carbonic acid and water exhaled at every breath are evidence of so much food and tissue consumed. This daily, hourly, momentary death of the tissues and destruction of food demand the constant renewal of the matters of which they are composed. Hence the necessity of food, by which I mean any substance, inorganic or organic, solid or liquid, that will nourish the body; renewing the material destroyed in producing the phenomena of life.

HUNGER AND THIRST.—The effects of withholding food entirely or of giving it in too small quantities are seen in cases of starvation and inanition.

Under ordinary circumstances the sensations of hunger and thirst are the first indications that solid and liquid food are required by the system. These sensations seem to be due to a certain condition of the stomach and mouth induced by the want of food experienced by the general system. That such is the case seems to be justified by facts like the following. It is well known that the sensations of hunger and thirst can be relieved by introducing food into the system through fistular openings made in the body by disease or wounds. Thus food taken into the system through an opening in the intestine, as is well known, will not only relieve the sensation of hunger but sustain life,<sup>1</sup> and in the case of an opening into the œsophagus, when water and spirit were injected into the stomach, the thirst was relieved.<sup>2</sup> It is also well known that bathing and wringing the clothes in salt water have been the means of temporarily relieving the thirst of shipwrecked sailors.

On the other hand, if the food is not absorbed, the sensations of hunger in the stomach and of thirst in the mouth are only temporarily relieved; even though solid food may be eaten and water be drunk in large quantities, the general wants of the system in such cases not being satisfied.

<sup>1</sup> Busch: Virchow's Archiv, 1858.

<sup>2</sup> Gairdner: Edinburgh Medical and Surgical Journal, 1820.



The consideration of death from hunger and thirst belongs rather to the subject of pathology. As an illustration, however, of how life depends upon waste, and of the manner and relative quantities in which the tissues are destroyed to maintain life, the records of death from want of food, solid and liquid, become of interest to the physiologist. For a starving man is living upon himself, and as nature is always economical in her expenditures, one may feel sure that the very best disposition possible under such circumstances is made of the material available in maintaining life. In the wasting away that takes place in these cases we have a guide as to the character of the nourishment that the system would have taken had food been supplied from without instead of from within, and can so deduce some conclusions as to the use of food generally.

Shipwrecks, prolonged sieges, imprisonments, forced marches, etc., furnish the data by which some idea may be obtained of the state of nutrition and of the agonies and horrors in cases of death from starvation. Among the symptoms of starvation may be mentioned, first, severe pain in the epigastrium, which usually passes away in a day or so, then an indescribable feeling of weakness, a sort of sinking, in the same parts is experienced. The face becomes pale and cadaverous, and there is a wild look in the eye. General emaciation follows, an offensive odor is noticed about the body, which is covered with a brownish secretion. The voice becomes weak, muscular effort is almost impossible, the intelligence can with difficulty only be aroused. Finally death takes place, usually in eight or ten days, often accompanied with mania and convulsions.

On post-mortem examination the most striking facts usually noticed are the diminution in the weight of the body, almost entire absence of fat and blood, and the loss in bulk of the most important viscera. The coats of the intestine are so thinned as to be almost transparent, the gall-bladder is distended with bile, and decomposition sets in very rapidly.

Death from inanition or insufficient food, though more prolonged than that from actual starvation, is essentially the same process only slower, being characterized by the same symptoms, and the same post-mortem changes. Many babies and young children in large cities and even in the country die from inanition—actually starved to death, undoubtedly through ignorance in some cases; but in others, however, the length of time in death from inanition varying so, and being often so extended, advantage is frequently taken of this to obscure and mask the true cause of death by those interested in escaping from the penalties of their criminal neglect of the children placed in their charge.

As already observed, one of the most prominent symptoms of starvation is the loss of weight. It may be generally stated that when this loss exceeds forty per cent., or from twenty to fifty per cent. according to Voit, of the weight of the body, death takes place.

TABLE XVI.--RELATIVE LOSS OF TISSUE IN STARVATION IN 100 PARTS.

|                                    | In doves, according to Chossat. <sup>1</sup> | In cats, according to Voit. <sup>2</sup> |
|------------------------------------|----------------------------------------------|------------------------------------------|
| Fat . . . . .                      | 93.3                                         | 97                                       |
| Blood . . . . .                    | 75.0                                         | 27                                       |
| Spleen . . . . .                   | 71.4                                         | 67                                       |
| Pancreas . . . . .                 | 64.1                                         | 17                                       |
| Liver . . . . .                    | 52.0                                         | 54                                       |
| Heart . . . . .                    | 44.8                                         | 3                                        |
| Intestines . . . . .               | 42.4                                         | 18                                       |
| Muscles . . . . .                  | 42.3                                         | 31                                       |
| Muscular coat of stomach . . . . . | 39.7                                         |                                          |
| Pharynx and œsophagus . . . . .    | 34.2                                         |                                          |
| Skin . . . . .                     | 33.3                                         | 21                                       |
| Kidneys . . . . .                  | 31.9                                         | 26                                       |
| Respiratory apparatus . . . . .    | 22.2                                         | 18                                       |
| Osseous system . . . . .           | 16.7                                         | 14                                       |
| Eyes . . . . .                     | 10.0                                         |                                          |
| Nervous system . . . . .           | 1.9                                          | 3                                        |

By looking at Table XVI., taken from the excellent works of Chossat and Voit, it will be noticed that the difference in the relative loss of the tissues is very considerable. Thus the nervous system loses only a little over one per cent., the muscles over forty per cent., while more than ninety per cent. of the fat disappears.

Now it has been noticed that in starvation the temperature falls, and most rapidly as death approaches; this is so evident that the immediate cause of death is undoubtedly cold. When it is remembered that one of the principal uses of the fatty principles is to produce heat through their combustion, the large loss of fat in such cases becomes intelligible, the animal using up its own fat as so much fuel.

Inasmuch as no food has been introduced into the body there is nothing for the economy to make blood out of, hence the small quantity found in the body after death from starvation. Further, what there is of it is of the most inferior quality, rather injurious than otherwise; for through the impeded circulation the worn-out and effete matters which are excreted and carried out of the system so rapidly in health accumulate in the stagnating inspissated fluid and represent so much poison.

Even though one should recover from the effects of long deprivation of food, the system for weeks afterward remains in a bad condition peculiarly favorable to the reception of any zymotic poison. Hence, from time immemorial, famine has been the harbinger, the forerunner of epidemics, the plague, etc. Almost invariably after a long siege, where there has been insufficient food, unless careful measures are taken, disease breaks out and carries off many of those spared by the sword. In the often-quoted words of Chossat, "inanition is a cause of death which advances in the front and in silence in every disease in which alimentation is not in a normal condition."

Terrible as the pangs of hunger are, those of thirst are worse. Man and animals will live longer without solid food than when deprived of water, man dying usually in a few days when no water at all has been

<sup>1</sup> Recherches Experimentales sur l'Inanition, p. 92. Paris, 1843.

<sup>2</sup> Hermann: Physiologie, Band vi. S. 97.



taken. When it is remembered that about three-fifths of the body consist of water this is readily accounted for.

The sensation of thirst, though caused by this general want of the system for water, is referred to the mouth and throat, which are first sensibly affected. These parts become very dry and hot and there is an agonizing feeling of constriction, fever sets in, the blood is very much diminished in quantity and becomes thickened, the urine is scanty and burns, the viscera may be said to be almost inflamed, delirium generally precedes death.

The importance of giving water freely, internally and externally, in health and disease cannot be too much insisted upon. No detailed argument is necessary to prove this point. The simple fact that sometimes within four days, even, men have died when entirely deprived of water speaks for itself.

There are cases sometimes mentioned of human beings who have lived for very long periods of time without eating or drinking anything. When the evidence of such cases, however, is examined critically it generally turns out (with some exceptions to be mentioned shortly) that a morsel of food or a little water has been taken at some time, and that the exceptions are usually only apparent.

USE OF FOOD.—We have seen that the body, both in health and starvation, wastes that it may live. The rate of waste, however, varies in different classes of animals, and in different individuals of the same species. Thus, mammals and birds, living a more active life than reptiles or batrachians, waste more tissue and food. A man who lives a fast life—using the term in its physiological sense—wastes more rapidly than one who lives a moderate one. Hence the difference in the amount and quality of the food required and the frequency in taking it observed in different animals, and by the same animal at different periods of its life. Thus the boa constrictor may feed only once in three or four months, while man eats, usually, three times a day.

Further, the food of the inhabitants of the polar regions, consisting principally of fatty, oleaginous principles, that of the people of tropical countries, of rice, dates, etc., shows that the food, in addition to repairing the waste of the tissues, fulfils other conditions essential to life.

Every one is sensible of the change of the seasons, feeling that icy winter is melting into spring, that budding spring is unfolding into summer. The traveller, journeying from temperate to polar or tropical regions, appreciates the increasing cold of the one, or heat of the other, and yet the average temperature of man remains about the same,  $98.6^{\circ}$  F., at all seasons, in all climates.

The temperature may rise as high as  $110^{\circ}$  in certain diseases, like tetanus, and even to  $122^{\circ}$  F., as in a case of injury to the spine, and <sup>18</sup> which may be mentioned, ended in recovery;<sup>1</sup> or, under certain conditions, may fall as low as  $83^{\circ}$  F., or lower, as in cholera. These extremes if maintained, however, are soon followed by death.

How can this constant heat in the human body be accounted for?

We have seen that the sugars and fats, and albuminous principles of

<sup>1</sup> Lancet, March 6, 1875.

which the body is composed, and which are derived from the food, are consumed in the economy, and produce heat. Thus food is so much fuel for the system. The question of some of the food being directly burnt up as such, as so much coal, or indirectly by first becoming tissue, and which has been already considered, does not affect the fact of the food being the source of heat to the economy.<sup>1</sup>

The use of food then is to repair not only the waste of the tissues, but also to supply the fuel for the production of heat and force. In the child, however, the food not only supplies these two wants, but also furnishes the materials for its growth, hence the large and constant amounts of food demanded by an active, healthy child. This fact should never be forgotten by the physician, for many persons seem to think that a child can be built up out of nothing. There is quite as much danger in giving a baby or child too little food as too much, for more of them die of starvation than of repletion.

Again, the food of the female during gestation, must furnish the materials out of which the child is developed, as well as supply her own wants. The food, under these circumstances, ought to be most generous, both in quantity and quality, that neither mother nor child should suffer.

Striking contrasts are offered, according to the particular use made of the food in one or more of the ways just mentioned by different classes of living beings, or of an animal at different periods of its existence. Thus in trees, making no muscular or nervous effort and, therefore, wasting but little, and having no constant temperature to maintain, all their food can be applied to increase their size, hence their indefinite growth. Insects, on the contrary, being most active, are usually small animals, the greater portion of their food being used up in producing their various actions, and little left for growth. In the foetal state of man the food is applied to growth, in the adult, for the purposes mentioned above; hence a man cannot grow indefinitely, his food being used for the development of mental and muscular force, there will be none left that can be appropriated for growth. Inasmuch as the quantity of food that can be taken by an animal is limited by the capacity of its alimentary canal, it might be inferred, *à priori*, that if the greater part of the food is applied to one particular use, there will be little or none left for any other.

Hot-blooded animals require more food than cold-blooded ones, in order to maintain their higher temperature, and their more active life. When hot-blooded animals, however, hibernate—that is, sleep for months at a time—they pass into a sort of cold-blooded state, taking no food, existing by living upon themselves: they always weigh less at the end of their sleep than at its beginning; the waste, however, is comparatively small, they living so quietly during the hibernating period.

By bearing in mind these facts, it becomes intelligible how individuals have been able to sustain life without taking food, water excepted, for many days beyond the period when ordinarily death from starvation

<sup>1</sup> The various conditions which influence the regulation and distribution of heat, and the cause of its production, will be deferred until we consider the subject of animal heat.



ensues. By taking little or no exercise, in passing most of the time in sleep, and residing in a tropical climate, or in a temperate one during the hottest summer months, while the experiment lasts, it will be found that the system needs but little food, the waste of the tissues being reduced to a minimum, and there being but little need for the heat produced on account of the high temperature of the surroundings. By living in this way, man can transform himself almost into a cold-blooded or hot-blooded hibernating animal. Under such circumstances he lives upon himself, and continually loses weight. When, as regards this loss of weight, a certain limit is reached, which varies according to the condition, previous mode of life, and peculiarities of the individual, he will certainly die of starvation unless food be taken, death from starvation being only a question of time if the system be deprived of food.

TABLE XVII.<sup>1</sup>—COMPOSITION OF BLOOD.

|                          |                                        |   |   |   |   |   |   |   |          |
|--------------------------|----------------------------------------|---|---|---|---|---|---|---|----------|
| Water                    | .                                      | . | . | . | . | . | . | . | 781.600  |
| Globulin                 | .                                      | . | . | . | . | . | . | . | 135.000  |
| Albumen                  | .                                      | . | . | . | . | . | . | . | 70.000   |
| Fibrin                   | .                                      | . | . | . | . | . | . | . | 2.500    |
| Serolin                  | .                                      | . | . | . | . | . | . | . | 0.025    |
| Cholesterin              | .                                      | . | . | . | . | . | . | . | 0.125    |
| Sodium                   | { Oleate<br>Margarate<br>Stearate }    |   |   | . | . | . | . | . | 1.400    |
| Potassium                | { Chloride }                           |   |   | . | . | . | . | . | 3.500    |
| Sodium                   | { Carbonate<br>Sulphate<br>Phosphate } |   |   | . | . | . | . | . | 2.850    |
| Magnesium                | { Sulphate<br>Phosphate }              |   |   | . | . | . | . | . | 0.550    |
| Free soda                | .                                      | . | . | . | . | . | . | . | 2.450    |
| Magnesium                | .                                      | . | . | . | . | . | . | . | 1000.000 |
| Calcium phosphate        | .                                      | . | . | . | . | . | . | . |          |
| Iron                     | .                                      | . | . | . | . | . | . | . |          |
| Extractives undetermined | .                                      | . | . | . | . | . | . | . |          |

KINDS OF FOOD.—At the conclusion of the last chapter it was stated that, as the principles of which the body is composed are derived from the blood, and the blood from the food, the same principles will be found in all three. By glancing at Table XVII., drawn up from Becquerel and Rodier, it will be seen that the blood contains water, sodium chloride, phosphates, fats, albuminous principles, etc., while any of the ordinary animal or vegetable foods, like fish, eggs, milk, flour, or potatoes, etc., will be seen from Tables XVIII. and XIX. to consist of essentially these same principles. Indeed, the food of man naturally divides itself, like the proximate principles, into three classes, the albuminous, carbohydrate, and inorganic. Liebig's classification into tissue-making and heat-producing food is correct, so far as in that some kinds of food

<sup>1</sup> Becquerel and Rodier : *Traité de Chimie, Pathologique*, p. 86. Paris, 1854.

are especially useful in producing heat. It must be remembered, however, that the combustion of all tissue produces heat, and that heat-making substances like fat, and the inorganic principles, make tissue as well as the albuminous ones. There is, therefore, no such sharp line of demarcation as heat- and tissue-making foods as Liebig's classification implies.

It may appear strange that inorganic principles like calcium phosphate, salt, water, etc., are classed as food, but as we have seen that the body is composed of inorganic as well as organic principles, we must regard as a food any substance that will furnish these principles. The chemical analysis of such substances as are seen in Tables XVIII. and XIX. explains why mankind makes use of eggs, fish, flour, potatoes etc., as food, these articles containing the inorganic and organic principles of which the body consists.

TABLE XVIII.<sup>1</sup>—ANIMAL FOODS.

| In 1000 parts | Mammals. | Birds. | Fish.  | Eggs.  | Milk.  |
|---------------|----------|--------|--------|--------|--------|
| Water . . .   | 728.75   | 729.83 | 740.82 | 735.04 | 861.53 |
| Albumen . .   | 174.22   | 202.61 | 137.40 | 134.34 | 39.43  |
| Collagen . .  | 31.59    | 14.00  | 43.88  | .....  | .....  |
| Fat . . . .   | 37.15    | 19.46  | 45.97  | 116.37 | 49.89  |
| Carbohydrates | .....    | .....  | .....  | .....  | 42.23  |
| Extractives . | 16.90    | 21.11  | 16.97  | 3.74   | .....  |
| Salts . . . . | 11.39    | 12.99  | 14.96  | 10.51  | 5.92   |

TABLE XIX.<sup>2</sup>—VEGETABLE FOODS.

| In 1000 parts   | Corn flour. | Peas (dried). | Potatoes. | Beet root. |
|-----------------|-------------|---------------|-----------|------------|
| Water . . . .   | 150.00      | ...           | 760       | 822.50     |
| Albumen . . .   | 132.50      | 280           | 10        | 20.40      |
| Starch . . . .  | 606.80      | 573           | 180       | .....      |
| Sugar . . . .   | 54.80       | ...           | ...       | 122.60     |
| Cellulose . .   | 26.60       | 76            | 40        | 25.60      |
| Fat . . . . .   | 16.80       | ...           | ...       | .....      |
| Salts . . . . . | 12.50       | 38            | 10        | 8.90       |

From the fact of the inorganic principles being usually combined in sufficient quantities with the organic, their indispensable use as food is often overlooked. The albuminous principles of the food that in the economy are converted into the albumen of the blood, are found both in the animal and vegetable foods. Thus we have albumen as musculin forming the basis of muscle, in various meats, beef, mutton, venison, lamb, etc., in the white of the egg, as casein in cheese, in birds, fish, oysters, and milk, as may be seen from Tables XVIII., XXI., and XXII.

In vegetables, albumen exists as vegetable albumen, readily converted into that of the blood. It is present in peas, potatoes, beets, flour, etc., as shown in Tables XIX. and XX.

<sup>1</sup> Moleschott, referred to by Carpenter, Principles of Human Physiology, 1881, p. 97.

<sup>2</sup> Carpenter, op. cit.



TABLE XX.<sup>1</sup>—COMPOSITION OF THE POTATO.

|                    |   |            |   |   |   |   |   |         |
|--------------------|---|------------|---|---|---|---|---|---------|
| Water              | . | .          | . | . | . | . | . | . . .   |
| Starch             | . | .          | . | . | . | . | . | . . .   |
| Albumen            | . | .          | . | . | . | . | . | . . .   |
| Gluten             | . | .          | . | . | . | . | . | . . .   |
| Fat                | . | .          | . | . | . | . | . | . . .   |
| Gum                | . | .          | . | . | . | . | . | . . .   |
| Asparagin          | . | .          | . | . | . | . | . | . . .   |
| Extractives        | . | .          | . | . | . | . | . | . . .   |
| Potassium chloride | . | .          | . | . | . | . | . | . . .   |
| Iron               |   |            |   |   |   |   |   |         |
| Manganeseium       |   | Silicates  |   |   |   |   |   |         |
| Aluminium          |   | Phosphates |   |   |   |   |   |         |
| Sodium             |   | Citrates   | } | . | . | . | . | . . .   |
| Potassium          |   |            |   |   |   |   |   |         |
| Calcium            |   |            |   |   |   |   |   |         |
| Free citric acid   | . | .          | . | . | . | . | . | . . .   |
|                    |   |            |   |   |   |   |   | 100.000 |

TABLE XXI.<sup>2</sup>—COMPOSITION OF OX FLESH.

|                                           |              |
|-------------------------------------------|--------------|
| Water . . . . .                           | 77.17        |
| Muscular fibre, vessels, nerves . . . . . | 15.80        |
| Tendinous tissue . . . . .                | 1.90         |
| Albumen . . . . .                         | 2.20         |
| Substances soluble in water . . . . .     | 1.05         |
| Substances soluble in alcohol . . . . .   | 1.80         |
| Calcium phosphate . . . . .               | 0.08         |
|                                           | <hr/> 100.00 |

TABLE XXII.<sup>3</sup>—COMPOSITION OF THE OYSTER.

|                         |   |   |   |   |   |   |   |   |   |   |         |
|-------------------------|---|---|---|---|---|---|---|---|---|---|---------|
| Water                   | . | . | . | . | . | . | . | . | . | . | 80.385  |
| Nitrogenized substances | . | . | . | . | . | . | . | . | . | . | 14.010  |
| Fat                     | . | . | . | . | . | . | . | . | . | . | 1.515   |
| Salts                   | . | . | . | . | . | . | . | . | . | . | 2.695   |
| Loss                    | . | . | . | . | . | . | . | . | . | . | 1.395   |
|                         |   |   |   |   |   |   |   |   |   |   | 100.000 |

Starch is found in vegetables, in greater proportions, for example, in wheat, corn, rice, potatoes, beans and peas, etc., than in turnips, cabbages, cauliflowers. Sugar is derived from animals, as milk and liver sugar, and sugar of honey; and from vegetables as cane and grape sugar. Fats and oils are found both in the animal and vegetable foods. By looking at the above Tables the relative proportions of the carbohydrate to the albuminous principles in the substances usually used as food may be seen, and the large quantity of water and constant presence of salts are especially noticeable.

Of the salts, amounting in twenty-four hours to about twenty grammes (three hundred grains), the most widely distributed are the sodium chloride and calcium phosphate, these being present both in the vegetable and animal foods. Iron, a most important principle, is found in eggs and milk. It is not necessary to dwell further upon the inorganic kinds of food, sufficient attention having been paid to them when treating of their use in the system as proximate principles.

<sup>1</sup> Pereira : Treatise on Food and Diet. New York, 1843.

<sup>3</sup> Payen : Substances Alimentaires, p. 221. Paris, 1865.

<sup>2</sup> Flint: Physiology, vol ii. p. 71.

## CHAPTER V.

### QUALITY AND QUANTITY OF FOOD.

It might be supposed from looking at Tables XVIII. and XIX. that it was immaterial whether man lived upon animal or vegetable food, since they both contain essentially the same substances, and this would receive confirmation when it was remembered that while many savage tribes on the one hand subsist almost entirely upon meat, the food of others on the other consists principally of the date, rice, etc., with little or no animal food. As a matter of fact, life can be sustained on either an animal or vegetable diet, the processes of digestion converting indifferently the albumen into albuminose, whether it be derived from beef or potatoes, and assimilating the fats and salts whether they are furnished by fish or bread. Living upon either animal or vegetable food, alone, however, is far from being an economical mode of diet, at least under ordinary circumstances.

It might be naturally inferred from the fact of man possessing at the present day incisor, canine, and molar or grinding teeth, that from time immemorial he had been accustomed to live on both kinds of food, for had he limited himself to one or the other, certain teeth would have probably disappeared or at least have become smaller through disuse. Diminution in size has actually taken place in the posterior molar teeth through the effects of eating cooked food.

The alimentary canal of man, as we shall see, is not so long or complicated as that of the herbivora, and yet not so simple as that of the carnivora, being rather a mean between the two. A fair conclusion from this comparison would be that a mixed diet is better adapted to the human system than an exclusively animal or vegetable one. The chemistry of the excretions not only confirms this view, but offers the explanation why it should be so.

TABLE XXIII.<sup>1</sup>

|                                                                                   |                   |            |  |
|-----------------------------------------------------------------------------------|-------------------|------------|--|
| 4600 grs. of carbon to 300 grs. of nitrogen in excreta, or 15 C to 1 N.           |                   |            |  |
| 30,000 grs. of bread contain 9000 grs. of carbon to 300 nitrogen, or 30 C to 1 N. |                   |            |  |
| 46,000 grs. of meat contain 4600 C, 1380 N, or 3 C to 1 N.                        |                   |            |  |
| about 2 lbs. of bread contain                                                     | C 4630 grs.       | N 154 grs. |  |
| “ $\frac{3}{4}$ lb. of meat contains                                              | C 463 grs.        | N 154 grs. |  |
| <hr/>                                                                             |                   |            |  |
| “ $2\frac{3}{4}$ lbs. of bread and meat contain                                   | C 5093 grs.       | N 308 grs. |  |
| or                                                                                | C 16 grs. N 1 gr. |            |  |

In a state of health there are found in the excreta for one grain of nitrogen fifteen grains of carbon (Table XXIII.). If a man should

<sup>1</sup> Carpenter: Physiology, 1881, p 96.



confine himself to vegetable food, say bread, for example, for every grain of nitrogen that he ate he would take in not only fifteen grains of carbon, that are necessary, but fifteen grains too much; in eating meat alone, while he obtains the one grain of nitrogen, he gets only about three grains of carbon, twelve grains too little. He must eat, therefore, nearly five times as much meat as is necessary, so far as the amount of nitrogen is concerned, in order to get the fifteen grains of carbon, and in so doing he loads his system with five times too much nitrogen. In eating bread you get twice as much carbon as is needed, and in eating meat four times too little. In diminishing the amount of bread you get too little nitrogen, and in increasing the amount of meat too much. If, however, the bread and meat are taken together in proper proportions we will get, according to the above calculation, the ratio of 16 of carbon to 1 of nitrogen in the excretions, which differs but little from that actually found, 1 to 15, and which can be accounted for by remembering that the food of man consists not only of bread and meat, but of other substances containing carbon and nitrogen.

Of the chemical elements entering into the composition of food, carbon and nitrogen are the most important with reference to the comparison to be made hereafter between the ingesta and the egesta in the determination of the origin of the latter, the source of animal heat, etc. The various methods adopted by chemists for determining the composition of foods will be found in the standard general and special treatises pertaining to that subject. It may be mentioned, however, incidentally here, that the determination of the carbon, hydrogen, and nitrogen entering into the composition of food is essentially accomplished by burning the substance in suitable apparatus, and of so converting its carbon, hydrogen, and nitrogen into carbonic acid, water, and ammonia, and of deducing the amounts of carbon, hydrogen, and nitrogen in the food examined from the carbonic acid, water, and ammonia produced, the remainder giving the amount of oxygen. Should the food contain sulphur and phosphorus in addition to the other elements just mentioned, their amount can be similarly determined by their conversion into sulphuric and phosphoric acids respectively. Table XXIV. gives the amount of carbon, hydrogen, nitrogen, etc. in the daily food.

TABLE XXIV.<sup>1</sup>

|                |             | C   | H  | O   | N  | S |
|----------------|-------------|-----|----|-----|----|---|
| Albuminoids,   | 130 grammes | 70  | 10 | 29  | 20 | 1 |
| Hydrocarbons,  | 300 "       | 134 | 18 | 148 |    |   |
| Fat,           | 100 "       | 76  | 12 | 12  |    |   |
| Mineral salts, | 20 "        |     |    |     |    |   |
| Water,         | 2000 "      |     |    |     |    |   |
|                |             | 280 | 40 | 189 |    |   |

The study of the teeth, alimentary canal, and the excretions explains what experience teaches, that generally a mixed diet is best adapted to

<sup>1</sup> Dalton, 7th ed., 1882, p. 132.

the wants of man. There are circumstances, however, when although the diet, strictly speaking, is mixed, it consists to a great extent of either animal or vegetable foods; the external condition being such that the wants of the system are better supplied by the one than the other.

<sup>tn</sup> Thus the Guachos in South America, spending their life in the saddle, and the climate being hot, live upon beef, there being little necessity for taking heat-making food, enough heat being generated through the combustion of the beef indispensable as supplying the force and replacing the tissue wasted in their active life.

The people inhabiting the Arctic regions, living in a temperature where the thermometer falls lower even than  $-40^{\circ}$ , would freeze to death were it not for the oily matters that are found in the whales and seals serving as articles of food, and which in their combustion produce so much heat. In tropical countries, however, the demand for carbonaceous food is at its minimum, the heat being intense, hence, the principal food consists of rice, etc., which contains relatively little carbon.

The obvious corollary from the above facts is, that travellers should accustom themselves as soon as possible to eat the food of the country they may happen to be passing through, and not invariably try to stick to the diet they have been accustomed to at home. Further, as the seasons change in any one particular place, the diet should be altered. Fats and sugars are more needed by the system in January than in July, and more exercise being taken in winter than in summer, tissue is wasted in this way in addition to that consumed to produce heat. The food should differ, therefore, both in quality and quantity in cold and hot weather.

This subject of food is of great importance to the practical physician, for improper food is a fertile source of disease.

The bilious diarrhoeas so common in the autumn are undoubtedly efforts of nature to relieve the system of the superfluous material that has accumulated in the system during the summer to such an extent that it can not be burnt up. The liver diseases that foreigners contract in the tropics are due, probably, to the same cause. An excess of albuminous food gives rise to gravel, gout, etc., through the imperfect combustion of the urates.

Rheumatism, etc., seems to be due to acidity resulting from the modification of the starch and sugars of vegetable food taken in too large quantities. A deficiency of oil on the one hand, and of fresh vegetables on the other, produces phthisis and scurvy respectively. In such cases the treatment is simply to diminish the article in excess and to supply that which is deficient.

The benefit derived from cod-liver oil in consumption is well known, and the improvement in gouty disease through entire change of diet and mode of life is often marked.

Theory and practice both agree, therefore, in showing that food must consist of a proper mixture of albuminous, oleaginous, saccharine, and saline principles, and just in proportion as any single food contains these principles will it be nutritious as an article of diet when used alone. The potato, for this reason, is invaluable as a food, containing as it does so many different substances, Table XX. Bread has been



called the staff of life, it entering so largely into the food of all classes of society. Table XXV., giving the composition of flour, explains

TABLE XXV.<sup>1</sup>—COMPOSITION OF FLOUR.

|                   |              |
|-------------------|--------------|
| Water . . . . .   | 2.25 ounces. |
| Gluten . . . . .  | 2.00 "       |
| Albumen . . . . . | 0.25 "       |
| Starch . . . . .  | 9.50 "       |
| Sugar . . . . .   | 1.00 "       |
| Gum . . . . .     | 0.25 "       |
| Fat . . . . .     | 0.125 "      |
| Fibre . . . . .   | 0.25 "       |
| Ash . . . . .     | 0.25 "       |
|                   | <hr/>        |
|                   | 15.975 "     |

why it fulfils the wants of the system to so great an extent. But "man cannot live by bread alone," and experience has shown that this is true of any one article of food; the disgust and loathing when restricted to one article of diet for any length of time becoming so intense that animals will even starve rather than touch the food under such circumstances.

Indeed, it is not only impossible for a man to subsist for any length of time upon a meat diet, but a carnivorous animal, a dog, for example, whose alimentary apparatus is especially adapted to the digestion of meat, soon succumbs when fed upon pure flesh alone, unless the body be well supplied with fat, an albuminous diet being in fact the same as a starvation one in which, as we have seen, the man or animal lives upon the flesh and fat of the body. On the other hand, if the food consists of fat alone, man or beast will live but a short time, and it is worthy of mention that on such a diet less urea is excreted than in the starving condition, the albuminous tissues, the source of the urea, being spared through the oxidation of the fat. If more fat, however, be taken than can be disposed of in this way, as shown by the retention of carbon in the system, then fat is stored up and the albuminous tissues destroyed. The effect of a carbohydrate diet is essentially the same as a fatty one, sugar or transformed starch being, however, more readily oxidized than fat, seventeen parts of sugar being equal to ten parts of fat in this respect; less urea is, therefore, excreted upon a carbohydrate diet than upon a fatty one. A certain amount of body fat appears to be also destroyed upon a carbohydrate diet.

Of all foods, milk (Table XXVI.) is the one which combines in itself to the greatest extent the proper substances in quantity and quality for the nutrition of the body, and were life limited to its early periods, we might say that milk is an exception to the rule just stated, but as the child develops into the adult necessity is felt for other kinds of food as well. All through life, however, milk constitutes a most important article of diet, and can be more relied upon, both in sickness and in health, than any other kind of food.

<sup>1</sup> Lankester Guide to the Food Collections in the South Kensington Museum, p. 39.

TABLE XXVI.<sup>1</sup>—COMPOSITION OF COW'S MILK.

|                                          |              |        |
|------------------------------------------|--------------|--------|
| Water . . . . .                          |              | 86.40  |
| Nitrogenized substances . . . . .        |              | 4.30   |
| Lactose . . . . .                        |              | 5.20   |
| Butter . . . . .                         |              | 3.70   |
| Calcium                                  | } phosphate  | 0.25   |
| Magnesium                                |              |        |
| Ferric                                   | } chloride } | 0.15   |
| Potassium                                |              |        |
| Sodium                                   |              |        |
| Sodium phosphate                         |              |        |
| Sodium lactate                           |              |        |
| Traces of coloring and aromatic matters. |              |        |
|                                          |              | 100.00 |

The quantity of food that a man can eat and live, is very different from that which he should eat. Mentioning incidentally that a young Esquimaux is said to have eaten thirty-five pounds of food, including tallow candles, in twenty-four hours, and a Hindoo a whole sheep at a time, and that Cornaro lived for fifty-eight years on only twelve ounces of vegetable matter and fourteen ounces of light wine, and Thomas Wood for eighteen years on sixteen ounces of flour made into a pudding with water<sup>2</sup> (a very exceptional case), let us ascertain, if possible, what is the proper amount of food for the average man in twenty-four hours.

According to Prof. Dalton,<sup>3</sup> "the entire quantity of food required during twenty-four hours, by a man in full health and taking free exercise in the open air, is as follows :

TABLE XXVII.—FOOD REQUIRED IN 24 HOURS.

|                         |                          |
|-------------------------|--------------------------|
| Meat . . . . .          | 453 grammes (16 ounces). |
| Bread . . . . .         | 540 " (19 " ).           |
| Butter or fat . . . . . | 100 " (3½ " ).           |
| Water . . . . .         | 1530 " (52 fluidounces). |

"That is to say, rather less than two and a half pounds of solid food and rather over three pints of liquid." It is desirable, indeed necessary, if health is to be maintained, that such articles as fresh vegetables, tea, coffee, milk, sugar, and fruit should be added from time to time to those just mentioned.

It will be observed from a comparison of Tables XXIII. and XXVII., that on a bread and meat diet more bread is eaten than when oil is also taken with them as part of the daily food. In the latter case the oil supplying part of the carbon, less bread is required.

TABLE XXVIII.<sup>4</sup>—DAILY RATION OF THE UNITED STATES SOLDIER.

|                                         |            |
|-----------------------------------------|------------|
| Bread or flour . . . . .                | 22 ounces. |
| Fresh or salt beef . . . . .            | 20 "       |
| Pork or bacon . . . . .                 | 12 "       |
| Potatoes (three times a week) . . . . . | 16 "       |
| Rice . . . . .                          | 1.6 "      |
| Coffee (or tea 0.24 oz.) . . . . .      | 1.6 "      |
| Sugar . . . . .                         | 2.4 "      |
| Beans . . . . .                         | 0.64 gill. |
| Vinegar . . . . .                       | 0.32 "     |
| Salt . . . . .                          | 0.16 "     |

<sup>1</sup> Payen : Substances Alimentaires, p. 139. Paris, 1865.<sup>3</sup> Physiology, p. 97.<sup>2</sup> Carpenter's Physiology, p. 114.<sup>4</sup> Physiology, vol. ii. p. 126. Flint.



Prof. Flint considers the United States army ration, Table XXVIII., as the most generous in the world. "The bread, meat, and potatoes contain 9.28 of carbon and 4.68 of nitrogenized matter, in addition to which are the alimentary principles contained in the rice, beans, sugar, and coffee, with the peculiar stimulant effect of the coffee."

According to Payen,<sup>1</sup> the soup used in the great Paris hospitals, and which is very nutritious, may be appropriately mentioned here as serving also as a guide in forming a diet scale for charitable institutions generally. Its composition may be seen from Table XXIX.

TABLE XXIX.<sup>2</sup>—FORMULA FOR MAKING SOUP.

|                                                         |                        |
|---------------------------------------------------------|------------------------|
| Water . . . . .                                         | 20 gallons.            |
| Meat with bones . . . . .                               | 68 lbs 10 oz.          |
| Vegetables . . . . .                                    | 13 " 10 "              |
| Salt . . . . .                                          | 1 " 12 $\frac{3}{4}$ " |
| Burnt onions (baked in oven until desiccated) . . . . . | 0 " 7 $\frac{1}{4}$ "  |

In concluding this general account of the subject of food, it may be stated that the effects of cooking food are three: First, to make it more palatable; second, to utilize it thoroughly; third, to improve its digestibility. Food which is agreeable to the taste is eaten with more relish; and, therefore, better digested than if unpalatable. If the food were not cooked, much of it would be unfit to eat and wasted, and even if it could be eaten much would be undigested.

There are a number of substances which cannot be regarded as food in the same sense as those already referred to, but as they are consumed to an enormous extent, in one form or another, by the majority of mankind, some reference must at least be made to them in this connection. I refer to tea and coffee, tobacco, distilled and fermented liquors.

TEA AND COFFEE.—As the composition and principal actions of tea and coffee are the same, they may be studied together. Tea and coffee are obtained from the *Thea chinensis* and *Coffea Arabica*, the tea and coffee plant respectively. As seen from Table XXX., they are composed of the same principles, united in different proportions.

TABLE XXX.<sup>3</sup>—COMPOSITION OF TEA AND COFFEE.

|                              | Tea.   | Coffee. |
|------------------------------|--------|---------|
| Water . . . . .              | 5      | 12      |
| Theine . . . . .             | 3      | 1.75    |
| Casein . . . . .             | 15     | 13      |
| Gum . . . . .                | 18     | 9       |
| Sugar . . . . .              | 3      | 6.5     |
| Tanic acid . . . . .         | 26.25  | 4       |
| Aromatic oil . . . . .       | 0.75   | 0.002   |
| Fibre . . . . .              | 20     | 35.048  |
| Fat . . . . .                | 4      | 12      |
| Mineral substances . . . . . | 5      | 6.7     |
|                              | 100.00 | 100.000 |

The active principles are usually distinguished as theine and caffeine. These alkaloids, however, and the active principle of the

<sup>1</sup> Substances Alimentaires, p. 101.<sup>3</sup> Carpenter: Physiology, 1876, p. 120.<sup>2</sup> Flint, op. cit., p. 87.

Paraguay tea, made from a shrub, have the same chemical compositions ( $C_8H_{10}N_4O_2 + 2H_2O$ ).

In making good tea there are usually allowed "one spoonful for each person and one for the pot," so each person gets then say about 100 grains of tea. We see, however, from Table XXX., that the quantity of theine, the active principle of tea, amounts to only three per cent.; it must be admitted, therefore, that its nutritive powers, either as a tissue- or heat-making food, must be very small. How account, therefore, for the value of tea as an article of diet, as daily experienced by hundreds of millions of people? The explanation of the effect of tea depends upon the fact of its increasing the amount of carbonic acid expired, and of waste; as first shown by Mr. Edward Smith.<sup>1</sup> Tea is a respiratory stimulant, and therefore powerfully promotes "those vital changes in food which ultimately produce the carbonic acid to be evolved." Instead, therefore, of supplying nutritive matter, it causes the assimilation and transformation of that already taken. The effect is not proportionate to the quantity of tea taken, and in this respect it is analogous to the action of a ferment. The sense of ease in respiration and increase of general comfort after taking tea are well known, as is also the fact that tea tends to induce perspiration and thereby to cool the body. Hence, in reference to nutrition, we may say that tea increases waste, since it promotes the transformation of food without supplying nutriment, and increases the loss of heat without supplying fuel. It is better adapted, therefore, to those who are well fed than to the poor and fasting.

The effects of tea upon the mind are well known: wakefulness, clearness and activity of thought, disposition for muscular exertion, etc. The exhaustion and nervousness which sometimes follow the excessive use of tea appear to be due to the loss of sleep and waste of tissue rather than to any poisonous action of its active principle. The effects of coffee and tea, in many respects, are the same. Coffee, however, differs from tea by diminishing the action of the skin. It lessens also the loss of heat of the body, but increases the *vis a tergo*, and, therefore, the heart's action and the fulness of the pulse, and excites the mucous membranes. The conditions, therefore, under which coffee may be taken are very different from those suited to tea. It is more suited than tea for the poor and feeble. It is also more fitted for breakfast, inasmuch as the skin is then active and the heart's action feeble, whilst in good health and with sufficient food it is not needful after dinner, but if then drunk should be taken soon after the meal.

It was formerly stated that the action of coffee, tea, etc., was an exception to the rule that increased vital activity is accompanied by waste, these substances being said to increase force but to diminish waste, the urea, which diminishes under the use of coffee, being supposed to be the measure of tissue change. It is now known that the emission of carbonic acid by the lungs is rather the true measure of muscular exertion, and this being increased by coffee and tea, the objection just mentioned is no longer of weight.

<sup>1</sup> Philosophical Transactions, 1859.



**TOBACCO.**—As the employment of tobacco is most extensive in all classes of society, a few words on its effect upon the system in this connection appear appropriate. The active principle of tobacco is a poisonous alkaloid, nicotia, consisting of  $C_{10}H_{14}N_2$ . The results of Dr. Hammond's experiments seem to show that under the use of tobacco the elimination by the kidneys of the uric and phosphoric acids is increased, but that the feces and urine are diminished, the exhalation of carbonic acid being only slightly affected. While the excessive use of tobacco no doubt produces a state of wakefulness, trembling, and nervous excitement, it cannot be denied that when moderately used it is often very beneficial, quieting and soothing the nervous system when exhausted by bodily and mental effort, and even in ordinary circumstances producing a general tranquillizing effect.

Tobacco seems also to promote digestion, stimulating the secretion of the gastric juice, perhaps by reflex action, hence the common custom of smoking a cigar after breakfast or dinner.

**ALCOHOL.**—Before considering the use of wines, malt liquors, and spirits, it is necessary to learn, if possible, the effects of pure alcohol upon the human body, since this principle is contained in large or small quantities in all such fluids. Alcohol chemically consists of  $C_2H_6O$ , and the first question to be investigated is, What becomes of it when taken into the system? Some experimenters, like Anstie and Dupre, found very little alcohol in the excretions, it appearing to be oxidized, burnt up; according to others, however, like Percy, Lallemand, Perrin, and Ducroy,<sup>1</sup> alcohol is found in the ventricles of the brain unchanged, and is eliminated by the lungs, skin, and kidneys.

It is possible that these contradictory results may be due to the different amounts of alcohol given, to the length of time that it has been in the system, and that under certain circumstances it is in part consumed and in part excreted. In either case, however, alcohol can be of no benefit to the system, for if it is found as such untransformed in the organs or excreted unchanged, it cannot supply any want, simply passing through the system, and if it is burnt up it must interfere with the oxidation of other substances, such as fat, etc., which under ordinary circumstances would, through combustion, disappear. If this view be correct, we have an explanation of hard drinkers becoming often so fat, the alcohol being burnt in preference to their fat, and so allowing their fat to accumulate in the muscles, in the liver, heart, etc., or, what is more likely, the alcohol in some way interferes with that splitting of food or tissue that normally precedes its oxidation.

Alcohol can never substitute the natural drink of man, water. Many substances which are soluble in the latter are precipitated by the former, and, hence, useless to the system; further, it does not supply any principle to the tissues.

Alcohol, in diminishing the amount of urea excreted and the action of the skin, and in interfering with natural combustion, perverts the whole nutrition of the body. The active changes and the rapid removal of the effete matters, so characteristic of healthy life, are retarded by

<sup>1</sup> Carpenter's Physiology, 1876, p. 107.

alcohol; hence, the susceptibility to zymotic poisoning of the dram drinker and his chronic diseases. It is well known also that less food is taken when alcohol is used, and so alimentation is affected. It is often urged that alcohol "will keep the cold out," but as the cutaneous vessels dilate under the use of alcohol through paralysis of the vaso-constrictor nerves more blood, and therefore more heat, comes to the surface, which instead of being retained within the body as it would otherwise be, escapes, the natural effect of the cold being to contract the vessels and of so keeping the heat in the body. Whether this be the true explanation or not, the fact remains the same, that Arctic voyagers keep the cold out far better without the use of alcohol than with it.<sup>1</sup> Finally, in addition to these facts, when it is remembered that many persons preserve their mental and bodily health perfectly without ever touching alcohol, it is difficult to offer a single good physiological reason for the use of alcohol at any time, the body being in health.

It must not be forgotten, however, that almost every people, savage or civilized, use alcohol in some form or another. Whether some, as yet unknown, want is supplied to the system by alcohol, or whether it is used merely to drown sorrow or to relieve ennui, is an undecided question. Among civilized people life is so artificial and man is so harassed bodily and mentally that, unfortunately, perfect health is far from being common. Life at times becomes weary, the heart feels oppressed, digestion is sluggish, the circulation impeded, muscular languor is present, then alcohol is useful, for it is a nervo-muscular stimulant. The action of the heart is accelerated, the blood flows more rapidly, the heart is relieved, and good results from its use. Every physician knows that in those dark hours when life hangs upon a thread, ~~that~~ <sup>8/</sup> alcohol is often the only remedy that has dragged the poor sufferer out of the jaws of death—the good effects of its temporary action bridging over such critical periods. As a medicine, alcohol is indispensable; when used for any other purpose, little or nothing can be said in its favor.

The action of alcohol is different in many respects from tea or coffee. Alcohol narcotizes the sympathetic, tea and coffee excite the cerebro-spinal nervous system; the former stupefies, while the latter brightens the intellect; the one inebriates and destroys, the other cheers and preserves.

**DISTILLED LIQUORS, WINE, MALT LIQUORS.**—The distilled liquors most commonly used are brandy, whiskey, gin, and rum. They contain, as a rule, a little more than 50 per cent. of alcohol, and hence, when abused, their bad effects. Brandy, the most valuable of them as a medicine, is obtained by the distillation of wine; whiskey from rye, wheat, etc.; gin, from different grains rectified by juniper, and rum from molasses. Brandy, whiskey, and gin diminish the amount of carbonic acid exhaled, and so interfere with vital processes. Rum, however, increases the carbonic acid exhaled, and, therefore, is less

<sup>1</sup> Hays: American Journal of the Medical Sciences, 1859.



hurtful in its effects. It has long been noticed that the rum-drinker lives longer than the brandy or gin-drinker.

TABLE XXXI.<sup>1</sup>—COMPOSITION OF WINE.

|                                                        |                 |
|--------------------------------------------------------|-----------------|
| Water.                                                 |                 |
| Alcohol.                                               |                 |
| Bouquet.                                               |                 |
| Sugar.                                                 |                 |
| Gum.                                                   |                 |
| Extractives.                                           |                 |
| Gluten (except where tannin is present).               |                 |
| Acetic acid.                                           |                 |
| Bitartrate of potassium.                               |                 |
| Tartrate of potassium and aluminium (in German wines). |                 |
| Sulphate of potassium.                                 |                 |
| Potassium and sodium chlorides.                        |                 |
| Tannin                                                 | } in red wines. |
| Coloring matter                                        |                 |
| Carbonic acid (in champagne).                          |                 |

Wine, or the fermented juice of the grape, is called full-bodied or light, according to the amount of alcohol present. There is always less alcohol in wines than in the distilled liquors just mentioned; thus port, Madeira, and sherry contain from 15 to 25 per cent. of alcohol; claret, sauterne, hock, about 10 to 15 per cent. In countries where the light wines are used by all classes of society, the horrible effects of spirituous liquors are almost unknown, the per cent. of alcohol being so small in light wines.

Wine, as seen from Table XXXI., contains, in addition to alcohol, sugar, gluten, and a number of salts, etc. Wine is nutritious in proportion to the amount in which these substances are present. In the preparation of many wines, like champagne, the amount of carbonic acid is increased; hence, their great use as diffusible stimulants in those cases where the vital powers demand prompt and active stimulation. Under such circumstances there is no better medicine than champagne.

TABLE XXXII.<sup>2</sup>—COMPOSITION OF BEER.

|                                  |        |
|----------------------------------|--------|
| Water                            | 947.00 |
| Alcohol                          | 4.50   |
| Dextrin, glucose, etc.           | 41.40  |
| Nitrogenized substances          | 5.26   |
| Mineral salts                    | 1.84   |
| Bitter principle not determined. |        |

---

 1000.00

Beer, ale, and porter are made from malted barley, with the addition of hops. All malt liquors contain alcohol; about 1 to 4 per cent. in the weaker, and from 6 to 8 per cent. in the stronger kinds. Even as much as 12 per cent. is found in the heavy English beers.

Table XXXII. gives the composition of the ordinary French beer,

<sup>1</sup> Pereira: A Treatise on Food and Diet, 1843, p. 502.

<sup>2</sup> Payen: Substances Alimentaires, p. 462. In the original table of Payen, 957 is given, instead of 947, probably a typographical error.

which will serve as an example of malt liquors generally. A most noticeable feature is the small amount of alcohol, and the very large quantity of glucose, etc. There are also nitrogenized substances, mineral salts, and a bitter principle. Apart from the alcohol they contain, malt liquors are nutritious on account of these carbohydrate and nitrogenized and inorganic principles. They are often of great service to persons who have run down, are debilitated, or who are slowly recovering from some exhausting, low type of disease, being taken then as medicine. In such cases the small quantity of alcohol in the malt liquor is beneficial, acting as a stimulant, the hops are useful as a tonic, and the remaining principles as food.

It will be seen from what has been said of alcohol that the evil resulting from the abuse of liquors of all kinds is proportional to the amount that is present of this principle, that malt liquors and light wines are less injurious than brandy and whiskey, and that beer, ale, etc., containing so many nutritious principles, closely approximate to the true idea of a food. The importance, however, of remembering that the malt liquors also contain alcohol, and in sufficient quantities to do mischief if too freely partaken of, will be appreciated when it is learned that 1,076,844,942 gallons of beer were consumed in 1873 in Great Britain, in addition, to spirits, wine, cider, etc.

Alcohol cost the United States, in ten years, directly, \$600,000,000; indirectly, \$600,000,000 more; destroyed 300,000 lives, sent 150,000 people to prisons and work-houses, 100,000 children to the poor-house, drove 1000 insane, determined 2000 suicides, caused loss by fire or violence of \$10,000,000 of property, made 200,000 widows, and 1,000,000 orphans.<sup>1</sup>

With such an array of figures it cannot be considered superfluous that attention has been called to the effect of alcohol in its relation with food.

<sup>1</sup> De Marmon : New York Medical Journal, December, 1870.



## CHAPTER VI.

### DIGESTION.

IN order that the food should fulfil its functions in the economy it must be assimilated, and before that can be accomplished the food must be first digested and then absorbed. Digestion should, therefore, be studied first.

Under the general term digestion are included several processes: the prehension of food, its mastication and insalivation, deglutition, the changes effected in the food during its passage through the stomach, the small and large intestine, and defecation.

While the various and often complicated ways in which the lower animals take their food are interesting to the comparative physiologist, the description of which would require a detailed account of the organs involved, it is unnecessary for me to dwell upon the simple process as observed in man. In sucking, however, it may be mentioned that this process is due to the tongue acting like a piston, since when the velum is applied to the back of the tongue and the mouth closed posteriorly a tendency to a vacuum is made, the lips at the same time closing around the nipples anteriorly. In drinking the action is essentially the same, except where the head, being thrown back and the liquid poured in, it is, so to speak, tossed off.

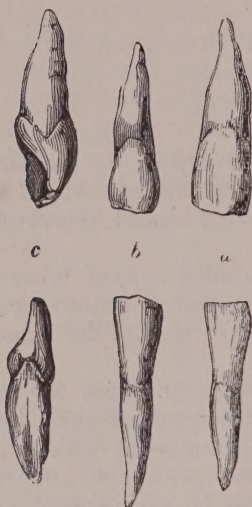
### MASTICATION.

The chewing of food, or mastication, is effected by the teeth, which, in the adult condition, are thirty-two in number, viz., eight incisors, four canines, eight premolars, and twelve molars. A tooth is usually described as having three parts. That portion which is seen in the mouth is called the crown. The tapering portion inserted in the socket, or alveolus of the jaw, is the root or fang, and is held in position by fibrous tissue continuous with the periosteum of the jaw and submucous tissue of the gum. The intermediate constricted part of the tooth between the crown and the fang is known as the neck, the accumulation of fibrous tissue at this position being called the dental ligament.

The incisor or cutting teeth (Fig. 16) four in each jaw, are nearest to the middle line in front of the jaw. They are inserted in their sockets by a single fang. The crown of the tooth is wedge-shaped, and presents a wide, sharp, and chisel-like edge, its lingual or inner surface is concave from above downward. In the upper jaw the central incisors are larger than the lateral ones, whereas, in the lower jaw the lateral are larger than the central ones. The incisors are well adapted to cut and bite the food.

The tooth next to the lateral incisors in both jaws is called the canine (Fig. 17), and corresponds to the large tearing and holding tooth in-

FIG. 16.



Incisor teeth of the upper and lower jaws. *a.* Front view of the upper and lower middle incisors. *b.* Front view of the upper and lower lateral incisors. *c.* Lateral view of the upper and lower middle incisors, showing the chisel shape of the crown; a groove is seen marking slightly the fang of the lower tooth. (QUAIN.)

called the stomach teeth. The canine teeth assist the incisors in dividing the food.

The premolars, two in each jaw (Fig. 18), succeed the canine. They are shorter and thicker than the latter. The crown is cuboidal, convex externally

FIG. 18.

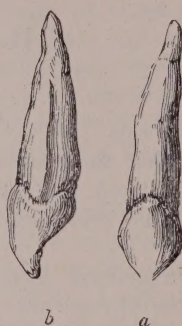


First bicuspid tooth of the lower jaw. *a.* Front view. *b.* Lateral view, showing the lateral groove of the fang and the tendency in the upper to division. (QUAIN and SHARPEY.)

and internally, and exhibits upon the triturating surface two eminences or cusps, hence their name of bicuspid. The fang is conical and flattened, and deeply grooved. The upper premolars are larger than the lower ones, and their fang is more or less subdivided into two.

The premolar teeth are succeeded by the twelve molar or grinding teeth, six in each jaw. The molar tooth (Fig. 19) has a cuboid crown. The triturating surface in the upper molars at the four angles is elevated into four tubercles with a diagonal ridge

FIG. 17.



Canine tooth of the upper jaw. *a.* Front view. *b.* Lateral view, showing the long fang grooved on the side.

the dog, and hence its name. The canine teeth, four in number, are larger than the incisor teeth. The crown is conical and bevelled behind, the fang is longer than in any of the other teeth, and laterally exhibits a slight furrow, as if indicating a tendency to subdivide into two. The upper canine or eye teeth are larger and longer than the lower ones. The latter are often

FIG. 19.



First molar tooth of the upper and lower jaws. They are viewed from the outer aspect. (QUAIN and SHARPEY.)

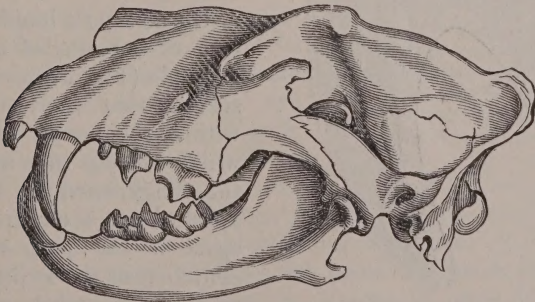


connecting two of them. In the lower molars there are five tubercles or cusps, two on the inner side and three on the outer. The upper molars are inserted in their sockets by a pair of conical fangs, the lower ones by three fangs, two external and one internal, the latter is the largest and grooved. The first molar tooth—that is, the one most anteriorly situated—is the largest, the third, or the wisdom tooth, the smallest. Often, however, in the savage races of mankind, in the milk teeth of civilized races, in the fossil man, and in the monkeys, the last molar is the largest. It is by means of the molar teeth that the food is crushed and ground up.

During mastication the external tubercles of the lower molars are opposed to those of the upper ones, and through the lateral motion of the lower jaw inward, the external tubercles pass down the inclined surfaces of the external ones and up those of the internal tubercles of the upper teeth, crushing the substances between them.

The teeth are arranged in the jaw somewhat in the form of a curve. In savage races, on account of the prominence of the canine teeth, the curve is rather of an oblong form, and in civilized races the curve is often V-shaped. The incisor teeth of the upper jaw overlap those of the lower, and the external cusps of the premolars and molar teeth close outside those of the lower jaw. It will be also observed that the central incisors of the upper jaw extend over the central and half of the lateral incisors of the lower jaw, whilst the upper lateral incisors come in contact with the outer half of the lower laterals and the anterior half of the lower canines. The canine teeth of the upper jaw extend over half of the lower canines and half of the lower first premolars. The first premolar of the upper jaw is opposed to the half of the first premolar and half of the second premolar of the lower jaw, whilst the second upper premolars impinge upon the posterior half of the second premolar and anterior half of the first molar of the lower jaw. The first molar of the upper jaw is opposed to the posterior two-thirds of the

FIG. 20.

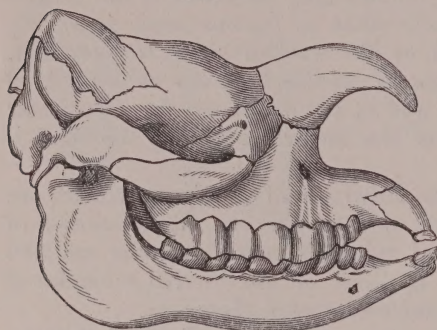


Skull of lion. (OWEN.)

first molar and anterior third of the second molar of the lower jaw. The second upper molar impinges upon the posterior third of the second and anterior third of the last molar of the lower jaw. The last molar in the upper jaw is opposed by that part of the third molar in the lower jaw which remains uncovered by the second upper molar.

By this disposition it will be seen that no two teeth are opposed to each other only, and that, with the exception of the last molar, each

FIG. 21.

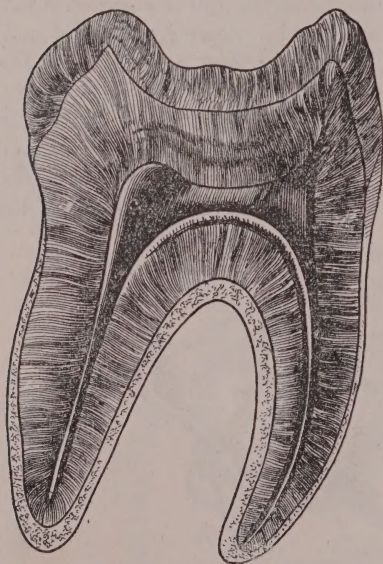


Skull of Indian rhinoceros. (OWEN.)

tooth in the upper jaw is opposed to two teeth in the lower one. If a tooth is lost, or even two alternate ones, the remaining teeth will therefore be still useful.

If the teeth of man be compared with those of a carnivorous animal, like a lion (Fig. 20), or with those of a herbivorous one, like a rhinoceros (Fig. 21), it will be noticed that in man the teeth are both of the carnivorous and herbivorous kinds, and pretty evenly developed, whereas, in the lion, on the one hand, the teeth are all of the biting, cutting, and tearing character; while in the rhinoceros, on the other hand, the largest teeth are of the grinding and crushing character. The teeth of the carnivorous lion and herbivorous rhinoceros are in harmony with the nature of their food.

FIG. 22.



Section of human molar tooth magnified (OWEN.)

One would infer from the fact of man possessing both incisor and molar teeth that his food had consisted from time immemorial of both animal and vegetable origin. This confirms what we have already learned from the chemistry of the food, that the diet of man should be a mixed one.

On making a longitudinal section of a tooth, of a molar for example (Fig. 22), it will be observed that there is a cavity within the crown of the tooth which extends into and through the fangs opening by a small aperture at their apices. This space is the pulp cavity, and contains, in the living tooth, the pulp. The tooth will be also seen from such a section to consist

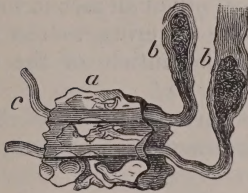
of three parts, dentine or ivory, a yellowish-white substance bordering the pulp cavity, enamel, a harder and whitish substance capping the crown, cement, a translucent bony-like layer encrusting the roots.

The dentine constitutes the great bulk of the tooth, chemically it consists of about twenty-eight parts of animal matter (tooth cartilage), and seventy-two of earthy salts, among the latter are principally found cal-



cium phosphate, some calcium carbonate and magnesium phosphate. When examined with the microscope dentine (Fig. 23) is seen to consist of an amorphous translucent matrix, in which are imbedded numerous canals or tubes, whose walls are distinct from the matrix. These latter are the dental or dentinal tubules, and average in diameter at their commencement  $\frac{1}{4500}$ th of an inch. The intermediate space between the adjacent tubules is about three times their diameter. The dental tubules open at their inner ends or beginnings into the pulp cavity, outwardly they pass to the periphery of the tooth. The tubules run generally in a parallel, but somewhat wavy course. As they pass outward they become gradually narrower, dividing and subdividing, giving off innumerable small branches,

FIG. 24.



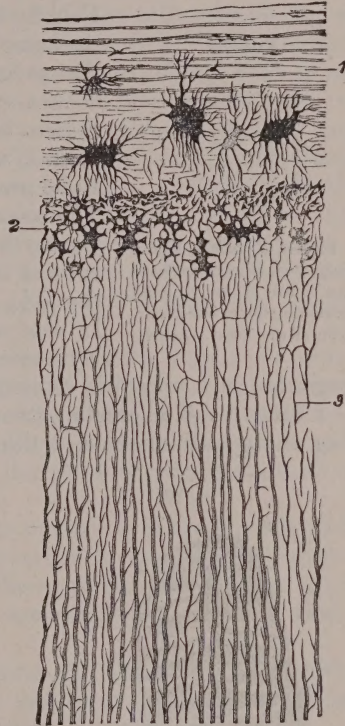
a. Dentine. b. Odontoblastic cells. c. Fibres.  
(TOMES.)

which anastomose or end blindly. Some of the terminal branches pass into the canaliculi of the cement, others into the so-called interglobular spaces, irregular cell-like cavities in the matrix. The walls of the dental tubules are about as thick as their calibre. In the living tooth the dental tubules are filled with the dental fibres, which are prolongations from the odontoblastic cells of the pulp (Fig. 24). These dental fibres are possibly the terminal filaments of the nerves supplying the tooth. The contour markings observed in the teeth are due to irregularities in the matrix or intertubular substance.

As age advances there is deposited upon the inner surface of the dentine a secondary kind of dentine, known as osteo-dentine, which resembles both dentine and bone. This appears to be due to a sort of ossification of the pulp, the effect of which is gradually to obliterate the latter and the pulp cavity.

ENAMEL.—The crown of the tooth is covered with the enamel, the hardest of organic substances. It is, however, gradually worn down by protracted use. The enamel is thickest upon that part of the tooth

FIG. 23.

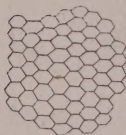


Section of fang, parallel to the dentinal tubules (human canine). Magnified 300 diameters. 1. Cement, with large bone-lacunae and indications of lamellae. 2. Granular layer of Purkinje (interglobular spaces). 3. Dentinal tubules. (WALDEYER.)

most used in trituration, here it exists in several layers; it is thinnest at the roots, where it gradually disappears.

Chemically, enamel consists of about five parts of animal matter, and ninety-five of earthy constituents, the latter being mostly calcium phosphate. Microscopically, enamel consists of solid six-sided prisms, the enamel fibres having an average diameter of  $\frac{1}{5000}$ th of an inch, and a length of  $\frac{1}{1000}$ th of an inch. Each prism rests by its inner end upon the dentine, the outer end being covered with the cuticle of the teeth.

FIG. 25.

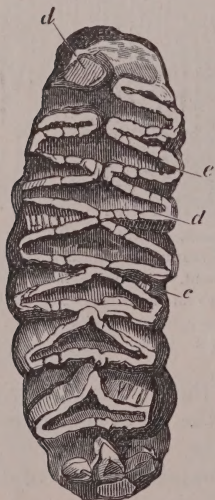


Section of enamel, highly magnified, at right angles to the course of its columns; exhibiting the six-sided character of the latter. (LEIDY.)

Usually there are several layers of enamel prisms, the outer layer being then covered with the cuticle. The prisms, while arranged in a parallel manner, do not run in an exactly straight direction, the course being rather an undulating one. The prisms, when viewed horizontally from their outer ends, present a tessellated appearance (Fig. 25). The so-called cuticle of the teeth, or membrane of Nasmyth, just referred to as covering the outer ends of the enamel prisms or fibres, averages about the  $\frac{1}{15000}$ th to the  $\frac{1}{30000}$ th of an inch in thickness. It acts as a protective covering to the enamel. By some histologists the cuticle of the teeth is regarded as a very thin cement.

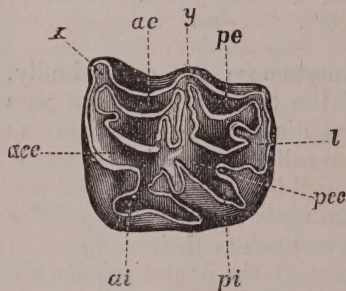
**CEMENT.**—The crusta petrosa or cement covers the roots of the teeth, beginning at the neck as a thin layer and becoming gradually thicker

FIG. 26.



Molar tooth of African elephant.  
e. Enamel. d. Dentine. c. Cement.  
(OWEN.)

FIG. 27.



Molar tooth of horse ae. Antero-external; pe. Postero-external; ai. Antero-internal; pi. Postero-external or principal cusps respectively. y. External vertical rib. x. An anterior cingular cusp. acc, pcc. Anterior and posterior cross-crests. (WORTMAN.)

at the fangs. It adheres very closely to the dentine and to the periosteal lining of the alveoli. Cement differs from bone in its lacunæ being more variable in their form and size, and their canicula being larger and more numerous. In many animals, like the cat, dog, and hog, the dentine, cement, and enamel are disposed as in man. In the grinding teeth of the herbivora, however, as in those of the elephant (Fig. 26), horse (Fig. 27), the dentine, enamel, and cement



alternate with each other in such a way that as the teeth are worn an uneven triturating surface is always maintained.

**TOOTH PULP.**—The pulp of the tooth situated in the pulp cavity is not only the formative organ of the tooth, but the source of its vascular and nervous supply; the tooth-pulp consisting of cells, bloodvessels, nerves, and a small quantity of connective tissue.

The cells are most numerous on the surface of the pulp. In this position they are known as odontoblasts and the layers formed by them as the *membrana eboris*. The odontoblastic cells exhibit three kinds of processes: Those passing internally into the pulp, others which serve to connect adjacent cells, and those already referred to as being prolonged into the dentinal tubules. The bloodvessels pass in and out by the openings in the apex of the tooth, forming beneath the odontoblastic layer a capillary network. The nerves enter by the fang of the tooth and after giving off a few branches form a plexus beneath the odontoblastic layer. The exact manner, however, in which the nerves terminate in the teeth is not known, unless, as already mentioned, the dental fibres are of a nervous character. The teeth of the upper jaw are supplied by branches from the superior maxillary nerve, those of the lower by the inferior maxillary.

No lymphatics, as yet, have been found in the tooth pulp, or in other parts of the teeth. As age advances, the pulp of the tooth diminishes in size through its gradual calcification, the odontoblastic layer atrophies, the connective tissue increases, the capillary network disappears, the nerves exhibit a fatty degeneration, and the pulp ultimately becomes a dried-up, insensitive mass.

Although the pulp may lose entirely its vitality, yet the enamel and dentine may remain serviceable, they appearing to be perfected structures. These are, however, never reproduced when destroyed by wear or decay or by loss of the tooth, with the rare exception of where a tooth is reproduced for the third time.

The way in which the teeth are developed and the manner in which the permanent teeth are preceded by the deciduous or milk set, will be considered under the subject of reproduction.

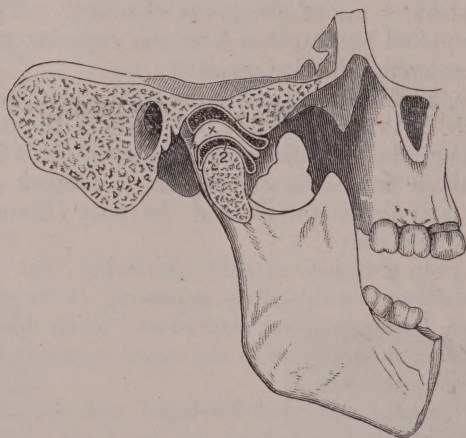
#### MAXILLARY BONES AND TEMPORO-MAXILLARY ARTICULATION.—

The teeth in man and mammalia are confined to the maxillary bones, in which they are imbedded, the bone being moulded so to speak, around the roots of the teeth after these are developed and so forming the sockets. Between the jaw and the tooth there is a space which in the living tooth is filled up by the alveodental periosteum. Through the elasticity of this root membrane the tooth possesses a certain amount of motion. Were the teeth immovably fixed in their sockets some shock would be felt during mastication. This alveodental periosteum, which passes imperceptibly into the gum and periosteum, consists of connective tissue in which are found nerves and vessels. There is also no sharp line of demarcation between the gum and the mucous membrane of the mouth on the one hand and the periosteum on the other.

Of the maxillary bones the superior, from being immovably articulated with the other bones of the head, are only passive in mastication. The upper teeth, however, offer fixed surfaces, against which those of the lower jaw are brought into apposition.

**INTERMAXILLARY BONE.**—If the inner surface of the superior maxillary bone be examined between the middle line and alveolar margin, in most instances a suture will be readily recognized running downward and outward from the anterior palatine foramen to the outer margin of the second incisor tooth. This suture is interesting from several points of view, among others, as indicating in the embryo the distinction existing between the true superior maxillary bones and the intermaxillary bones, the latter being characterized by carrying the incisor teeth. As development advances, however, in man and to a great extent also in monkeys, the superior maxillaries coalesce to such an extent with the intermaxillaries that the primitive distinction between the bones is almost entirely lost, in some instances the suture itself even disappearing. In the other mammalia, however, the intermaxillaries remain quite distinct from the superior maxillaries and each other, and are readily disarticulated. It was this latter circumstance that led Goethe,<sup>1</sup> equally

FIG. 28.

Antero-posterior section of the temporo-maxillary articulation of the right side. (A. T.)  $\frac{1}{8}$ . (QUAIN.)

great as a poet and naturalist, to look for and discover the intermaxillary bone in man, so convinced was he that the skull consisted of the same bones in all the mammalia.

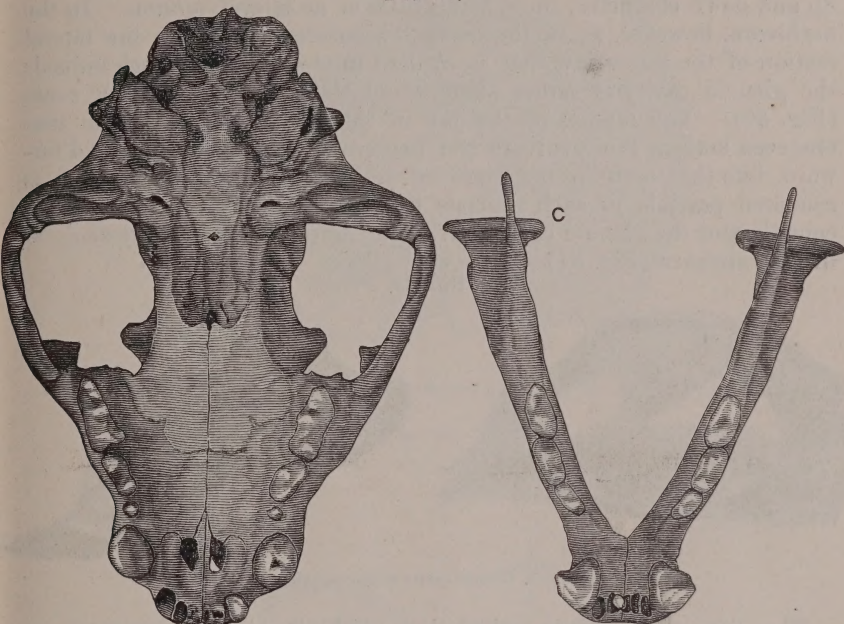
The inferior maxillary bone, mandible or lower jaw, consists in the adult of a single piece movably articulated with the temporal bone (Fig. 28). This articulation is really a double joint, since there is interposed between the condyle and the glenoid cavity a biconcave oblong piece of fibro-cartilage to the edges of which is attached the capsular ligament. The spaces on either side of the cartilage are lined with synovial membrane, and there is no connection between the two cavities unless the cartilage is perforated. When the jaw is simply depressed, the joint acts as a hinge. Through the movement of the condyle on the eminentia articularis, the forward and lateral motions of the jaw are affected. The mechanism of the temporo-maxillary articu-

<sup>1</sup> Sammtliche Werke, Band vi., Osteologie, S. 65.



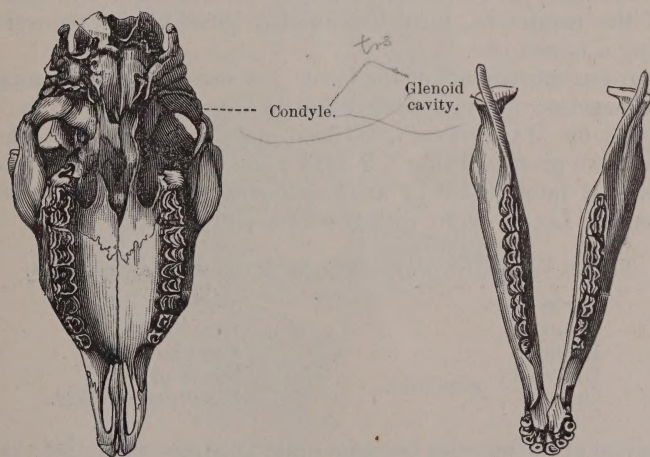
lation is therefore such as to insure great freedom of motion to the lower jaw. The lateral, forward, and depressing actions of the jaw either succeed each other or are variously combined during the mastication of food.

FIG. 29.



Jaws of tiger

FIG. 30.

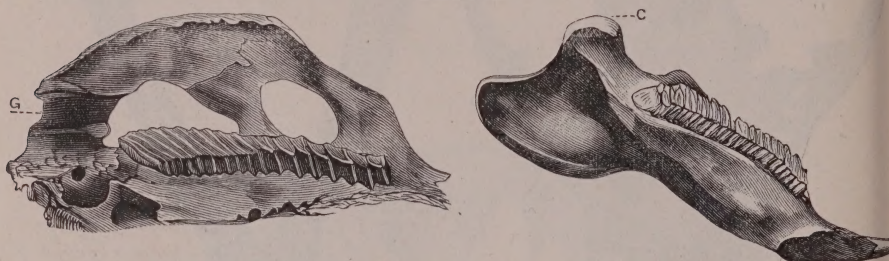


Upper and lower jaw of sheep. (OWEN.)

If the condyle of the jaw in a carnivorous animal be examined, in a tiger, for example (Fig. 29), it will be noticed that its long diameter is transverse, and that the glenoid cavity is grooved, hollowed out, so as

to receive it. This disposition is carried out to such an extent in the badger that the lower jaw will remain depressed, interlocked, within the glenoid cavity, even though all the ligaments be cut away. The motion of the lower jaw in many of the carnivora is almost exclusively of an up and down character, there being little or no lateral motion. In the herbivora, however, as in the sheep, rhinoceros, etc., it is the lateral motion of the lower jaw that is evident in chewing. In such animals the glenoid cavity is rather shallow and the condyle oblong or ovate (Fig. 30). The motion of the jaw in the rodentia differs from that observed both in the carnivora and herbivora, being backward and forward, like that seen in the gnawing action of a rat. This motion is rendered possible in such animals through the long diameter of the condyle and the glenoid cavity having an antero-posterior direction, as in the capybara (Fig. 31).

FIG. 31.



C. Condyle, and G. Glenoid cavity of the capybara. (TOMES.)

The temporo-maxillary articulation, combining in man, as we have seen, to a great extent, in one joint, the peculiarities just noticed in the temporo-maxillary articulation of the carnivora, herbivora, and rodent types of the mammalia, furnishes another proof of the natural diet of man being a mixed one.

The various movements of the lower jaw are effected by a number of different muscles; to the consideration of these let us now turn.

**MUSCLES OF MASTICATION.**—These muscles naturally divide themselves into two groups, Table XXXIII., one of which elevates the lower jaw, moves it laterally or in an antero-posterior direction; the other depresses it. Let us begin with the former group first.

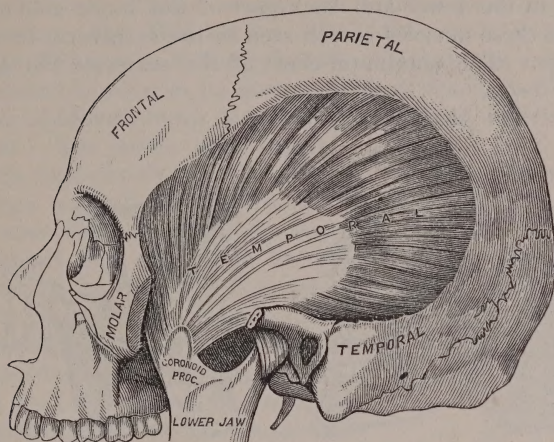
TABLE XXXIII.—PRINCIPAL MUSCLES OF MASTICATION.

| Elevators, etc. |              | Depressors.       |  |
|-----------------|--------------|-------------------|--|
| Temporal.       |              | Digastric.        |  |
| Masseter.       |              | Mylo-hyoid.       |  |
| External        | } pterygoid. | Genio-hyoid.      |  |
| Internal        |              | Platysma myoides. |  |

The action of the muscles becomes quite apparent when their anatomy is understood. The temporal (Fig. 32) arising from the temporal fossa and inserted into the coronoid process raises the lower jaw against the upper. The action of the temporal is aided by the contraction of the masseter and internal pterygoid, the former muscle (Fig. 33) arising from the zygomatic arch and passing backward into the lower border of

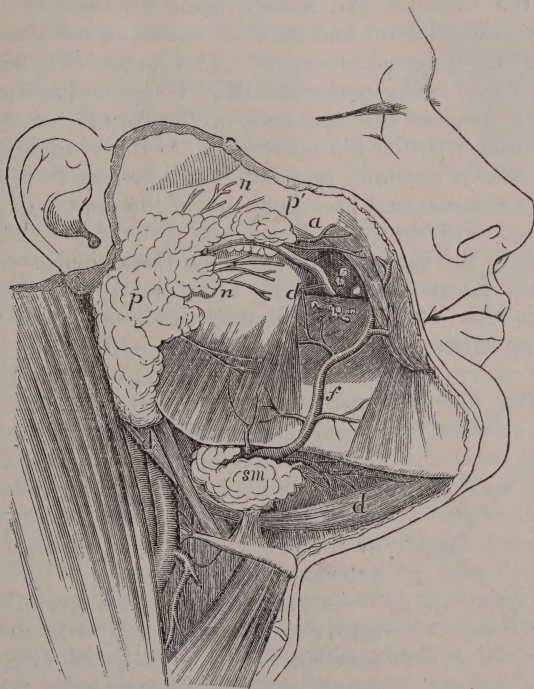


FIG. 32.



The temporal muscle, the zygoma and masseter having been removed. (GRAY.)

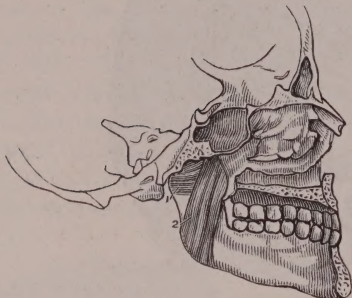
FIG. 33.



Sketch of a superficial dissection of the face, showing the position of the parotid and submaxillary glands (ALLEN THOMSON). Two-fifths the natural size. *p*. The main part of the parotid gland. *p'*. The small part, which lies alongside the duct, on the masseter muscle. *d*. The duct of Stenson before it perforates the buccinator muscle. *a*. Transverse facial artery. *n, n*. Branches of the facial nerve emerging from below the gland. *f*. The facial artery passing out of a groove in the submaxillary gland and ascending on the face. *sm*. Superficial larger portion of the submaxillary gland lying over the posterior part of the mylo-hyoid muscle. *d d*. Digastric muscle. (QUAIN and SHARPEY.)

the jaw, the latter (Fig 34) having its origin in the pterygoid fossa and its insertion in the lower and back part of the inner side of the jaw. The action of these muscles is well seen in the carnivora, in which they are very large. The maximum effect of the masseter can also be well

FIG. 34.



View of the pterygoid muscle from the outer side.  
 $\frac{1}{4}$ . 1. External pterygoid. 2. Internal pterygoid.  
 (QUAIN.)

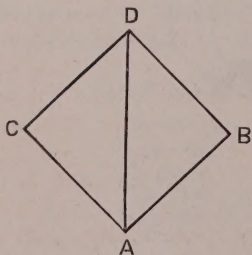
FIG. 35.



View of the pterygoid muscle from the inner side.  $\frac{1}{4}$ . 1. External pterygoid. 2. Internal pterygoid. (QUAIN.)

observed in the rodentia, the muscle being enormously developed in these animals. The lateral and forward motion of the lower jaw is due to the action of the external pterygoid. This muscle (Fig 35) arises from the sphenoid, palate, and superior maxillary bones, and passing backward and outward is inserted into the neck of the condyle of the lower jaw and into the inter-articular fibro-cartilage. If the condyle of the jaw on one side, the left for example, be fixed, it will be seen from the direction of the fibres of the external pterygoid that if the muscle of the opposite side contracts it will draw the lower jaw forward and laterally in an inward direction, the condyle playing upon the articular eminence, the cartilage being interposed, it having been also drawn forward by the muscle. This alternate lateral motion of the lower jaw is very evident in the chewing of the food, particularly well seen in the herbivora, in which order the external pterygoid muscle is relatively much developed. If the external pterygoids, however, act together, the lower jaw is drawn forward along the diagonal  $AD$  of the parallelogram, the two sides of which,  $AB$   $AC$  (Fig. 36), are the directions taken by the jaw when alternately acted upon by the external pterygoids.

FIG. 36.



As regards the second group of the masticatory muscles there can be no doubt as to the function of the mylo-hyoid (Fig. 37) genio-hyoid, and platysma myoides muscles. The two former muscles passing from the hyoid bone to the mylo-hyoid ridge and genial tubercle of the lower jaw respectively will depress the jaw when the hyoid bone is fixed. The same effect is produced by the platysma, it being partly inserted into the lower border of the jaw. The action of the digastric muscle is not so simple as that of the other

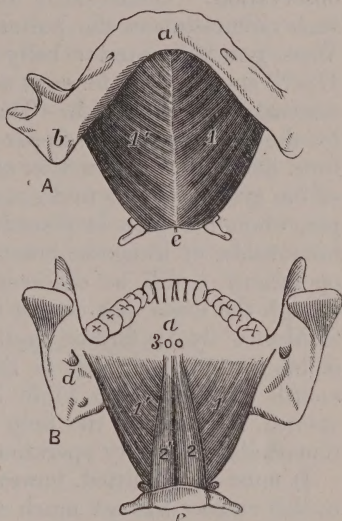


depressors; indeed, its action in depressing the lower jaw was denied by the elder Monro.<sup>1</sup> This view gave rise to his memorable discussion, in the last century, with Winslow,<sup>2</sup> in which Ferrein<sup>3</sup> later took part, who agreed with Winslow in holding that the digastric was a depressor.

The digastric muscle, as its name implies, is double-bellied, consisting of an anterior and posterior muscular part with an intervening tendinous portion. The tendon often passes through the stylo-hyoid muscle, gliding through a small synovial bursa,<sup>4</sup> "and is connected with the body and great cornu of the os hyoides by a broad band of aponeurotic fibres in the form of a loop and lined with synovial membrane."<sup>5</sup> The posterior belly of the digastric muscle passes upward, backward, and outward from the tendon to the digastric groove of the temporal bone, the anterior belly upward and forward to the inner surface of the jaw, near the symphysis. An interesting fact to be noticed is that the anterior belly is supplied by the mylo-hyoid branch of the inferior maxillary branch of the fifth nerve, the posterior belly by the facial, as we shall see when we come to study the nervous system; this shows that the muscle is essentially a double one.

Such being the disposition of the digastric muscle, it follows that if the jaw be fixed and the anterior belly alone contracts, the hyoid bone will be elevated anteriorly, as it is by the genio-hyoid and mylo-hyoid muscles in the first stage of deglutition. If, however, the posterior belly alone contracts, the hyoid bone will be raised upward and backward, its action being similar to that of the stylo-hyoid muscle. Should both bellies contract, then the hyoid bone will be elevated almost perpendicularly. On the other hand, should the hyoid bone be fixed by its depressor muscles, the lower jaw will be slightly depressed if the anterior belly of the digastric muscle acts alone; should the posterior belly act independently, then the mastoid process will be drawn downward, and with it the back of the head, thereby elevating the upper jaw and opening slightly the mouth. This action of the posterior belly alone, or with the anterior one acting with it, is no doubt aided by the deep muscles of the neck. While it is possible that the lower jaw can be depressed by

FIG. 37.



A. The lower jaw and hyoid bone, from below, with the mylo-hyoid muscles attached.  
B. The same from behind, with the mylo-hyoid and genio-hyoid muscles attached.  
(A. T.).  $\frac{1}{2}$ .

<sup>1</sup> Remarks on the Articulation, etc., of the Lower Jaw, p. 341. The works of Alexander Monro, M.D. Edinburgh, 1781. Also Medical Essays, 1733.

<sup>2</sup> Mem. de l'Acad. Roy. des Sciences, 1742, tome 59, p. 176.

<sup>3</sup> Ibid., tome xli. pp. 427, 509.

<sup>4</sup> Hyrtl: Lehrbuch der Anatomie, Elfte Aufl., S. 402.

<sup>5</sup> Quain's Anatomy, 8th ed., vol. i. p. 282.

the anterior belly of the digastric acting alone, it is most probable that the posterior belly acts with the anterior one in producing this effect, the muscle acting in the reverse direction of that just referred to producing the movement of the back of the head. This view is confirmed by the fact pointed out by Winslow<sup>1</sup> that in several animals the anterior belly of the digastric muscle is wanting, the posterior alone being present and being then inserted into the angle of the jaw. Owen<sup>2</sup> called attention to, this being the case in the orang, and the author has confirmed the observation.<sup>3</sup> Occasionally the anterior belly is absent in man. Under such circumstances the posterior is inserted into the ramus of the jaw. Were not the anterior belly normally present it is possible that, as Hyrtl<sup>4</sup> suggests, the forward and lateral movements of the jaw might be seriously interfered with. That the mouth is to a certain extent opened by the elevation of the upper jaw through the backward motion of the head due to the contraction of the posterior belly of the digastric and of the muscles of the neck, may be shown in various ways. For example, when the chin is placed upon a table, the lower jaw being then immovable, or when the lower jaw is firmly fixed, as in certain surgical operations, it will be observed that the mouth can be slightly opened, though the lower jaw cannot be depressed. The experiment suggested to Monro<sup>5</sup> by his former pupil, Pringle, of putting the blade of a knife or his own nail opposite to the conjoined edges of the teeth when the mouth is shut, which knife being held unmoved while the mouth is opened, he may, by the help of a mirror, see the upper teeth raised, remarkably, at every operation he performs," is very convincing.

It must be admitted, however, that the movement of the upper jaw in this respect has not much significance, as the opening of the mouth is essentially due to the depression of the lower jaw. Indeed, the movement of the upper jaw in the opening of the mouth was denied altogether by Winslow.<sup>6</sup> In this respect, however, Ferrein agreed with Monro, although the former attributed the action of the upper jaw to the digastric, the latter to the muscles of the neck.

Of the muscles of mastication, as we shall see hereafter, the temporal, masseter, pterygoid, mylo-hyoid, and anterior belly of the digastric are supplied by branches of the fifth pair of nerves; the platysma myoides and posterior belly of the digastric by the facial, and the genio-hyoid by the hypoglossal.

RÉSUMÉ.—The effect of mastication is that the solid food taken into the mouth is cut and crushed and ground up by the teeth. The little pieces that ooze out between the teeth and the cheeks are pushed under the teeth again by the muscular action of the cheeks and lips, while the fragments that escape within the inner side of the teeth are forced back by the tongue. The importance in man of the action of the cheeks, lips, and tongue in mastication is well seen when there is a paralysis of the facial or hypoglossal nerves. In such cases the food accumulates between the cheeks and the teeth, and the want of action of the tongue is seen both in the difficulty of mastication and deglutition. The same effect can be pro-

<sup>1</sup> Op. cit.

<sup>3</sup> Proc. Acad. of Nat. Sciences, Philadelphia, 1880.

<sup>5</sup> Op. cit., p. 239.

<sup>2</sup> Proc. Zool. Soc. Lond., 1830, p. 29.

<sup>4</sup> Topograph Anat., Fünfte Aufl., S. 438.

<sup>6</sup> Panizza: Gaz. Méd., 1835, p. 419.



duced by cutting the corresponding nerves in animals.<sup>1</sup> The thorough mastication of the food insures its further digestion. Indeed, a most fertile source of dyspepsia is the too common custom of bolting the food. In the latter part of the last century it was shown by Spallanzani<sup>2</sup> that different kinds of meat when enclosed in perforated tubes and so swallowed, passed through his alimentary canal comparatively undigested. When the meats, however, were first broken up and then placed within the tubes very little undigested matter was found in them when passed by the anus.

In granivorous birds, like the common fowl, for example, the want of teeth is supplied by pebbles swallowed with the food, the gizzard triturating the food by means of the pebbles.

Mastication should be kept up until the food is thoroughly ground up. The teeth are so exquisitely sensible to the presence of any hard matter that we are enabled by them to know at once whether the process of mastication is completed. During mastication not only is the food thoroughly triturated, but it becomes gradually incorporated with the saliva. To the consideration of the production and effects of this secretion let us now turn.

<sup>1</sup> Panizza : *Gaz. Méd.*, 1835, p. 419.

<sup>2</sup> *Fisica Animale et Vegetabile*, tomo secondo, p. 52. Venezia, 1782.

## CHAPTER VII.

### INSALIVATION AND DEGLUTITION.

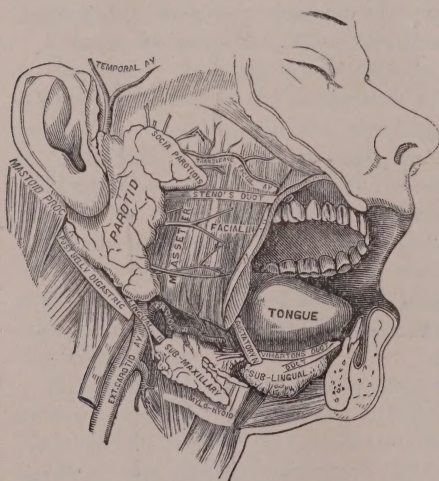
#### INSALIVATION.

THE saliva consists of a mixture of the secretion of the parotid, submaxillary, and sublingual glands, usually known as the salivary glands (Fig. 38), and also of the labial, buccal, lingual, molar, and pharyngeal glands. These glands are structurally examples of the racemose or grape-like type of gland, so called from the secreting portion of the gland with its efferent duct resembling a bunch of grapes attached to the stem (Fig. 39.)

The dilatations or diverticula from the duct are lined with cells in which the secreting power resides.

Let us now consider some of the peculiarities of the saliva secreted by these different glands. In man the secretion of the parotid is more

FIG. 38.



The salivary gland. (GRAY.)

FIG. 39.



Minute structure of a racemose gland of the parotid. (MILNE EDWARDS.)

abundant than that from any of the other salivary glands. Cases of salivary fistula occurring in man from time to time have given physiologists like Jarjarvay

Mialhe<sup>1</sup> the opportunity of examining, separately, the parotid saliva, while Dalton<sup>2</sup> and Schiff<sup>3</sup> have obtained it directly by introducing a tube into the duct of Steno. According to Dalton, the parotid saliva is alkaline, clear, and watery, which enables it to mix readily with and soften the food. Its flow is most active during mastication, about

<sup>1</sup> Berard : Physiologie, tome ii. p. 403, note. Paris, 1849.

<sup>2</sup> Physiologie de la Digestion, tome i. p. 183. Florence, 1867.

<sup>3</sup> Physiology, 1864, p. 125.



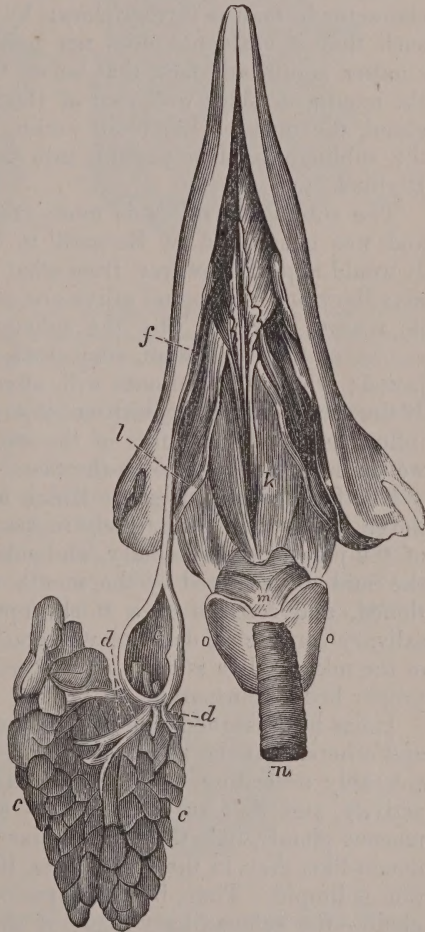
three times as much saliva being secreted on the masticating side of the mouth as on the opposite one. These facts, taken into consideration with that of the orifice of the duct of Steno being so situated that the saliva at once comes in contact with the food that is being masticated, suggest the view that the function of the parotid saliva is directly connected with that of mastication.

The facts of comparative physiology lead to the same conclusion. Thus, in the ruminantia, which chew their food very thoroughly, the parotid glands are very large; on the other hand they are usually absent in the cetacea, whales, dolphins, etc., and but little developed in the otter, seal, hippopotamus, the latter not needing parotid glands, the water in which they live or pass much of their time sufficiently moistening their food. Bernard<sup>1</sup> has also shown that if the duct of Steno be divided in the horse, the time required in chewing a feed of oats is three times as much as under ordinary circumstances. The food is also swallowed with difficulty under such circumstances, through the want of its proper admixture with the saliva. It is well known also that less saliva is produced in the horse on a feed of oats than on one of hay or straw, and that food already moistened excites little if any flow at all.

In experimenting upon animals, more particularly on dogs, Bernard noticing after inserting a tube into the duct of Wharton, and placing a sapid substance like pepper upon the tongue, that there was an abundant flow of submaxillary saliva, concluded that the function of this kind of saliva was connected with the sense of taste. To a certain extent this view is probably true.

Reflection, however, upon the relative development of the submaxillary glands in different kinds of mammals, in connection with the habits of the same, leads to the conclusion that one of the uses, at least, of the

FIG. 40.



Salivary gland and bladder, armadillo.

<sup>1</sup> *Physiologie Experimentale*, tome ii. pp. 49, 147. *Ibid.*, p. 74.

submaxillary saliva is that of a lubricating kind. Thus in the carnivora, in which the food is rather bolted than chewed, the submaxillary glands are large, whereas the parotids are small. In the great ant-eater, also, *Myrmecophaga jubata*, while the parotid gland is so small that it escaped even the notice of Cuvier, the submaxillary gland is sixteen inches in length and secretes an extremely viscid, tenacious saliva which lubricates the prehensile and extensible tongue, to which the ants adhere, ~~and~~ on which the animal subsists. The submaxillary glands are also very large in the armadillo and echidna (Fig. 40).

That the function of the submaxillary saliva is of a lubricating character in man is further shown by its viscosity, the consistence being such that it coats but does not penetrate the bolus of food; and by another significant fact, that before the submaxillary saliva passes into the mouth, it mixes with part of the viscid secretion of the sublingual gland, the duct of Bartholin joining the duct of Wharton, the rest of the sublingual saliva passing into the mouth directly by the ducts of Rivinus.

The sublingual saliva is more viscid, even, than the submaxillary, and was considered by Bernard<sup>1</sup> to be directly related to deglutition. It would appear, however, from what has been said, that both the submaxillary and sublingual saliva are connected in deglutition. There is no reason, however, why the submaxillary saliva should not be also connected with gustation, since insipid substances will be usually rejected; whereas, sapid ones will, after being tasted, be then swallowed. If the secretion aids deglutition, it is natural to suppose its flow will be influenced by the stimulus of the exciting sapid substance, ~~and~~ which we shall hereafter see to be the case.

The fluids secreted by the labial, buccal, or molar glands, etc., have never been studied separately in man. In animals in which the ducts of the parotid, submaxillary, and sublingual glands have been ligated, the fluid still secreted by the mouth comes from the glands just mentioned, and consists of a thick, opaque, grayish mucus, containing salivary corpuscles, desquamated epithelial cells, etc. The turbidness of the mixed saliva is due to this secretion, that from the salivary glands proper being transparent.

It has been learned from the researches of Heidenhain,<sup>2</sup> Lavdowsky,<sup>3</sup> and others, that the minute structure of the salivary glands differs considerably according as they are examined after a period of rest or activity, and that such differences are more marked in the so-called mucous glands, like the submaxillary, in which the secretion is viscid, mucin-like, than in the serous ones, like the parotid, in which the secretion is limpid. Thus, if, after a period of rest, a section of a "mucous" gland—the submaxillary gland of the dog, for example—be examined, the cells of an alveolus (Fig. 41, A) will be found to stain with carmine more readily in certain parts than in others. The nuclei and surrounding protoplasm, and the demilune cells—apparently young cells lying next to the basement membrane—become deeply tinged, while the

<sup>1</sup> Comptes Rendus, 1852, tome xxxiv. p. 237.

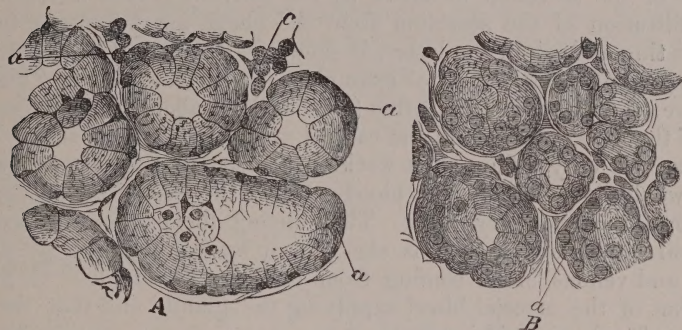
<sup>2</sup> Hermann: Physiologie, Funfter Band, S. 58. Leipzig, 1880.

<sup>3</sup> Archives of Mic. Anat., 1877, xiii. S. 281.



remaining portion of the cell remains uncolored, due apparently to its protoplasm in this situation having been converted into a mucin-like substance. If, however, similar sections of the gland be made after a period of activity induced by stimulation, as we shall see of the chorda tympani nerve, it will be observed (Fig. 41, *B*) that but a small portion,

FIG. 41.



Section of a "mucous" gland. *A*. In a state of rest. *B*. After it has been for some time actively secreting. *a*. Demilune cells. *c*. Leucocytes lying in the intervalveolar spaces. The darker shading in both figures is intended to indicate the amount of staining. (After LAVDOWSKY.)

if indeed any part, of the cell has resisted coloration with carmine, and that the cells have diminished in size.

If sections of a "serous" gland—the parotid gland of a rabbit, for example—after periods of rest and activity, be treated in the same way with carmine, differences of the same kind will be observed. Thus, after rest the cells of the parotid (Fig. 42, *A*) will be found to be pale, transparent, with few granules, staining by carmine with difficulty, the nuclei irregular in outline, apparently as if shrunk. After a period

FIG. 42.



Section of a "serous" gland: the parotid of the rabbit. *A*. At rest. *B*. After stimulation of the cervical sympathetic. (After HEIDENHAIN.)

of activity, on the other hand (Fig. 42, *B*), from stimulation by the sympathetic nerve, the cells will be seen to have become turbid, full of granules, staining readily with carmine, the nuclei large and round, with conspicuous nucleoli, and the cells, as a whole, smaller. Such facts lead us naturally to conclude that during a period of rest the cells of the salivary glands are elaborating from the blood their characteristic

secretion, the elements of the latter existing in the blood, but not the secretion itself, as such; that the secretion, as formed, is stored up (the part not staining with carmine) until needed, when at the proper moment it is forced into the interior of the gland and thence passes into the duct, the normal stimulus to the secretion being, as we shall see hereafter, impressions made upon the tongue, etc., and which are transmitted by the appropriate nerves supplying the glands. That the process of the secretion of saliva by the salivary glands is not one of mere filtration of the secretion from the blood, apart from the former not existing as such in the latter, is shown by the fact of the submaxillary secretion—of the dog, for example—passing into the duct under a pressure of about 200 millimetres (8 inches), or about twice as great as that of the blood-pressure in the carotid artery of the same side. Were pressure the only influence at work in the secretion of the saliva, the latter would flow back to the blood whence its elements came, rather than into the excretory duct. That during the process of secretion chemical action is going on, is also shown by the temperature of the saliva and venous blood coming from the gland being  $1.5^{\circ}$  C. higher than that of the arterial blood supplying the gland,<sup>1</sup> and that the production of carbonic acid is increased.<sup>2</sup>

Inasmuch as, under ordinary circumstances, it is the mixed saliva which modifies the food, it will not be necessary to dwell upon the chemical or physical peculiarities of any one particular kind of it.

TABLE XXXIV.—COMPOSITION OF HUMAN SALIVA.

|                         |   |           |   |   |   |   |   |   |   |         |
|-------------------------|---|-----------|---|---|---|---|---|---|---|---------|
| Water                   | . | .         | . | . | . | . | . | . | . | 995.16  |
| Epithelium              | . | .         | . | . | . | . | . | . | . | 1.62    |
| Organic matter, soluble | . | .         | . | . | . | . | . | . | . | 1.34    |
| Potassium sulphocyanide | . | .         | . | . | . | . | . | . | . | 0.06    |
| Sodium                  | } | phosphate | . | . | . | . | . | . | . | 0.98    |
| Calcium                 |   |           | . | . | . | . | . | . | . |         |
| Magnesium               |   |           | . | . | . | . | . | . | . |         |
| Sodium                  | } | chloride  | . | . | . | . | . | . | . | 0.84    |
| Potassium               |   |           | . | . | . | . | . | . | . |         |
|                         |   |           |   |   |   |   |   |   |   | 1000.00 |

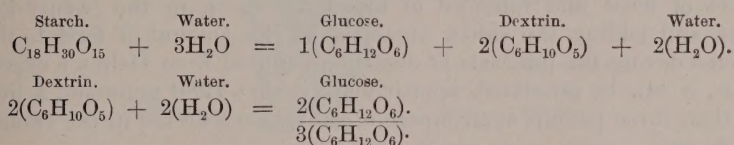
The saliva as we find it in the mouth, consisting then of a mixture of all the different kinds of saliva, is an alkaline, colorless, somewhat opaque, viscid fluid, with a specific gravity of from 1.004 to 1.006; its composition is given in Table XXXIV. Like all the secretions, the saliva consists largely of water, some organic matter, and a small quantity of salts. In 1831, Leuchs<sup>1</sup> discovered that hydrated starch, when mixed with warm saliva, was liquefied and converted into sugar. Since then, numerous experiments have been performed on animals, especially dogs, with the object of showing that their saliva has not this effect upon starch. While these observations are interesting from a general physiological point of view, they have no bearing whatever upon the question of the effect of human saliva upon starch. Anyone can convince himself that starch is converted into sugar in the mouth by

<sup>1</sup> Ludwig and Spiess: Sitz. d. Wiener, Acad. Math. Nat. Classe, 1857, xxv. S. 548.

<sup>2</sup> Pflüger: Pflüger's Archiv, 1868, Band i. S. 686.



taking a little boiled starch, mixing it thoroughly with his saliva, and then testing for sugar. The mixture will not then give a blue color on the addition of iodine, but at first a red or violet one, showing that the starch has become partly dextrin; the latter is, however, soon also transformed into glucose or grape sugar, as can be shown by Trommer's test. Saliva has the same effect on raw starch, only a longer time is required to produce it. It has been ascertained by experimenting with the different substances entering into the composition of the mixed saliva, that it is a portion of the albuminous organic matter which possesses this transforming effect, and that the different kinds of saliva have, as well as the mixed saliva, the property of converting starch into sugar. The phenomenon appears to be one of fermentation with hydration, as may be seen from the following reaction :



The action appears to be due to a kind of ferment, the so-called ptyalin of Berzelius, which can be isolated by precipitation by alcohol, the exact nature of which, however, at present is not thoroughly understood. According to Mialhe<sup>1</sup> one part of ptyalin will effect the transformation of more than two thousand parts of starch. It will be seen from this that its action must be very energetic. Nevertheless, as the large quantity of starch present in the food remains but a short time in the mouth, it is questionable whether any great amount of it is converted into sugar in the mouth, notwithstanding the admitted rapidity of the action of the saliva. We shall see, however, that the transforming effect of the saliva upon starch is continued even after the food has passed into the stomach, the gastric juice not interfering with the action, and, as the food remains for some time in that organ, no doubt a considerable quantity of sugar is produced there in this manner.

The importance of the saliva, however, in this respect, must not be exaggerated, as we shall see that the intestinal and pancreatic juices transform starch into sugar as efficiently as the saliva, and it is well known that the serum of the blood, mucus, the fluid from cysts, etc., have the same property, though not in as great a degree as the fluids first referred to. The significance of the potassium sulphocyanide, which appears to be always present in the saliva, is not apparent. The remaining salts, while rendering the saliva alkaline, have not been shown as yet to serve any particular purpose in digestion.

While one of the uses of the saliva in man is certainly the transformation of starch into sugar, undoubtedly its most important function is that of aiding mastication and deglutition, the secretion of the parotid gland being specially connected with the former function, that of the submaxillary and sublingual glands with the latter, as we have seen in speaking of the secretions separately. The amount of saliva secreted

<sup>1</sup> Chimie applique a la Physiologie, p. 43. Paris, 1856.

during twenty-four hours in man has never been exactly determined. As the saliva is constantly being reabsorbed, a source of error in any calculation as to the amount secreted in a given time would be the risk of counting the same saliva, or, at least, the elements entering into its composition more than once. According to Dalton,<sup>1</sup> 31.1 grammes, about 478 grains, of saliva can be obtained from the mouth in twenty minutes without any artificial stimulus. The natural stimulus to the secretion of the saliva, however, is the presence of food in the mouth; indeed, the sight, or even the thought of food, in some individuals will make the mouth "water." The amount of saliva secreted will depend, therefore, on the quantity and quality of the food. According to Dalton,<sup>2</sup> wheaten bread will gain during mastication fifty-five per cent. in weight, lean meat forty-eight per cent. Assuming that about sixteen ounces of meat and nineteen of bread are eaten in the twenty-four hours, and adding the saliva absorbed by this amount of food to that secreted during the intervals of digestion deduced from Dalton's experiments, it can be estimated, approximately, that 1280 grammes, a little less than three pounds avoirdupois, of saliva are secreted in the twenty-four hours.

After the food has been thoroughly masticated and mixed with the saliva, the secretion of the parotid gland penetrating the bolus, while that of the submaxillary, sublingual, and remaining glands of the mouth rather coating it externally, it is swallowed. As the bolus of food passes down the pharynx it receives another coating from the secretions of the glands in that situation, and so deglutition is further facilitated. In concluding our account of the saliva there may be mentioned appropriately in this connection the peculiarity it possesses of attracting or entangling bubbles of air in the mass of food. The effect of this is that stomach digestion is facilitated through the easy access afforded to the gastric juice when the food comes in contact with this secretion. Moist, heavy bread is not readily acted upon by the secretions, through its not being permeated with air in the manner just referred to. Let us now consider the manner in which deglutition is effected.

DEGLUTITION.—The act of swallowing, or deglutition, is often divided arbitrarily by physiologists into three stages or periods, though these stages are strictly continuous. During the first stage the food passes backward to the isthmus of the fauces. The second stage is occupied by the passage of the food through the palate from the isthmus into the œsophagus; while the third stage consists in the food passing from the œsophagus into the stomach. After the food has been thoroughly chewed, the mouth being closed, the first stage of deglutition begins by the tongue, more especially its point aided by the cheek, collecting the particles of the food into a mass or bolus. Through the action of the hyoglossal muscles (Fig. 43) the tongue is then moved forward and upward; the effect of this is that the bolus of food is pressed against the hard palate, and thence into the fauces, through the tongue being somewhat elevated at the sides and depressed in the centre, while the soft palate is applied at the base probably. Probably some slight suction

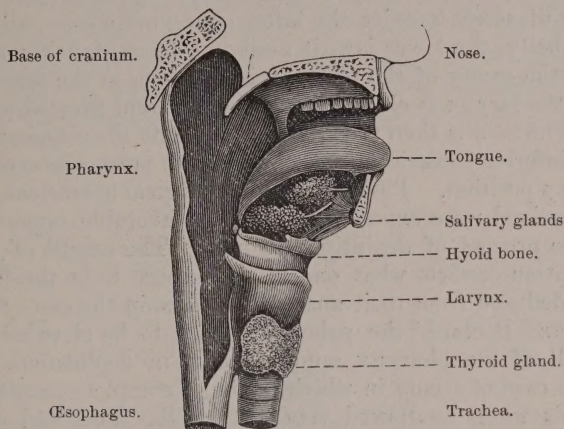
<sup>1</sup> Physiology, 1882, p. 144.

<sup>2</sup> Op. cit., p. 146.



force is exercised in the swallowing of liquid and soft articles during the first stage of deglutition.

FIG. 43.

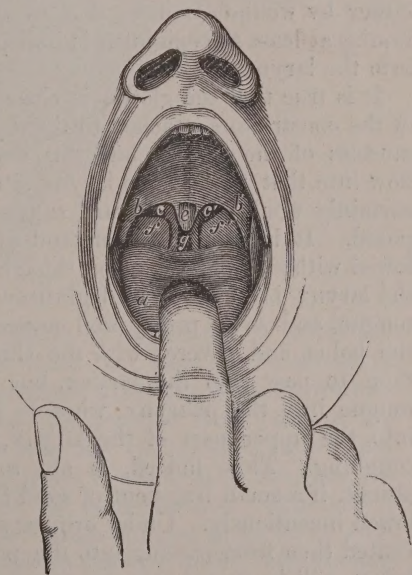


Vertical section of mouth and pharynx. (MILNE EDWARDS.)

The tongue is as important in deglutition as we have seen it to be in mastication. The results of dividing the hypoglossal in animals, already referred to, and the cases observed in man where the tongue has been amputated, or congenitally deficient, show that without the action of the tongue deglutition is impossible.

In amputation of the tongue there is usually left a portion of the base sufficient to press against the palate, making deglutition possible. The action of swallowing during the first stage is usually performed unconsciously; in reality, however, it is a voluntary one. As the food passes through the fauces, the tongue being drawn upward and backward by the contraction of the stylo-glossal muscles the entrance to the fauces is thereby narrowed, then the posterior half arches of the palate approach each other through the action of the palato-pharyngeal muscles, while the interval between them is filled up by the uvula (Fig. 44), at the

FIG. 44.



e. Uvula. b b. Anterior half arches. c c. Posterior half arches. f f. Tonsils. (VALENTIN.)

same time the soft palate is rendered tense by the tensor palati and elevated by the levator palati; the natural communication between the pharynx and posterior nares being then cut off, the food passes from the isthmus of the fauces into the pharynx, the superior constrictor of

which grasps the bolus of food and the soft palate. The pharynx, in the meantime, is elevated with the larynx through the contraction of the stylo-pharyngeal, stylo-hyoid, genio-hyoid, mylo-hyoid, probably the thyroïd and the digastric muscles, the latter acting more especially through its anterior belly, the lower jaw, it need not be said, being now fixed. In this way the cavity of the pharynx is widened, at the same time the entrance to the larynx is closed, being elevated and pressed against the epiglottis. The food is then forced downward into the œsophagus by the middle and inferior constrictors, after which the parts concerned resume their ordinary position. Pathological and surgical operations, in which the parts involved were exposed, have given favorable opportunities of observing the process of deglutition in man. The results of such clinical investigation confirm what one might expect to be the function of the parts as deduced from their anatomy. Thus, in the cases referred to by Berard,<sup>1</sup> and Beclard,<sup>2</sup> the palate was seen to be elevated while the posterior wall of the pharynx approached it in deglutition. Berard<sup>3</sup> mentions the case of a lady in which, through complete paralysis of the velum, liquids when swallowed returned by the nose, and cites, also, as an illustration of the elevation of the palate in deglutition, the experiment of Debrou, in which a probe being introduced along the floor of the nares into the pharynx, it was observed that every time the patient swallowed the external end of the probe was depressed, the internal end being elevated by the palate. Numerous cases, among others those cited by Longet,<sup>4</sup> in which the epiglottis has been destroyed in man, either by wounds or disease, show very conclusively that in swallowing liquids at least the epiglottis is indispensable in preventing them flowing into the larynx.

It is true that the glottis is closed in deglutition, both by the action of the constrictors attached to the thyroid cartilages and by the intrinsic muscles of the larynx, but this does not explain why liquids do not flow into that part of the larynx situated above the glottis, which they certainly would do as Berard suggests, unless some obstacle was interposed. It is easy to understand why, usually, solid food can be swallowed without difficulty, even though the epiglottis be deficient, as when the larynx is elevated in deglutition it rises up under the base of the tongue, and so is pretty well covered. The food being moulded into the bolus, and covered with the slimy, viscid saliva, would not be apt, then, to pass into the larynx, but would glide over the base of the tongue into the pharynx, whereas liquids would insinuate themselves into the upper part of the larynx, and at once give rise to a fit of coughing. This, indeed, is apt to take place, the epiglottis being absent, if a small fragment of solid food, a crumb, for example, be swallowed incautiously. Under ordinary circumstances, the food being prevented then from passing into the posterior nares above and the larynx below, will be forced into the œsophagus. At that moment the third stage of deglutition begins. The action of the œsophagus is very simple, consisting in the contraction of its circular and longitudinal muscular fibres from above downward, by which action the food is forced into the stomach (Fig. 45).

<sup>1</sup> Physiologie, tome ii. p. 25.

<sup>3</sup> Op. cit., pp. 24, 25.

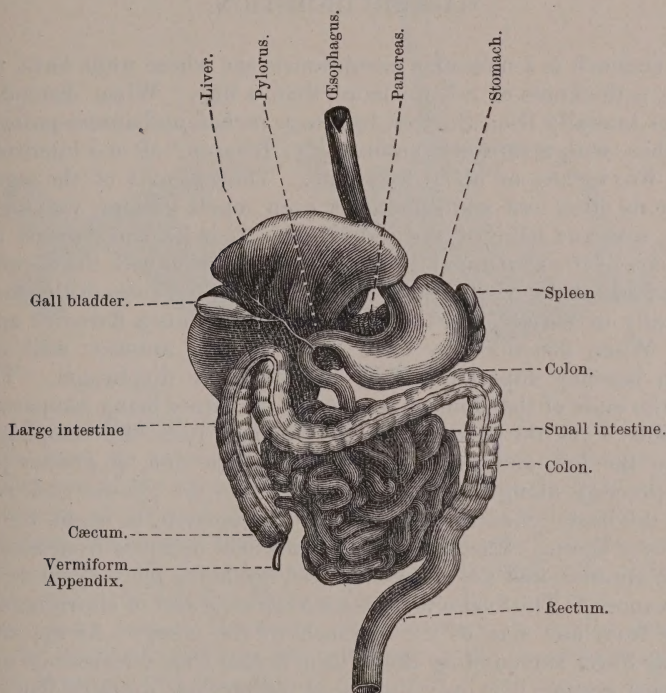
<sup>2</sup> Physiologie Humaine, p. 60.

<sup>4</sup> Physiologie, 1861, tome i. p. 115.



A peculiarity about the muscular fibres of the œsophagus is in the upper portion consisting exclusively of striated fibres, whereas, in the lower part unstriated fibres predominate. This disposition of the fibres is interesting, as accounting, probably, for the fact of the lower third of the œsophagus remaining contracted for a short time after the food has passed into the stomach, thereby preventing regurgitation. This phenomenon was particularly observed first in animals by Magendie.<sup>1</sup>

FIG. 45.



Digestive apparatus of man. (MILNE EDWARDS.)

While, as has been stated, the first period of deglutition is under the control of the will, the second and third are entirely involuntary, depending, as we shall see when we come to study the nervous system, upon an impression being made upon the mucous membrane of the pharynx and œsophagus, etc., which sets the appropriate nerves and muscles in action. Indeed, without solid or liquid food in the pharynx it is impossible to perform the second act of deglutition; apparently, this is done sometimes for three or four times without there being anything to swallow, but there is really always present under such circumstances sufficient saliva to produce the necessary impression.

It is hardly necessary to call attention to the fact that solid and liquid foods can be swallowed in all positions. It is a common feat among jugglers to drink a bottle of wine or a glass of beer while standing on their heads or hands.

<sup>1</sup> Mémoires sur l'Œsophage, à l'Institut de France, 11 Oct. 1813.

## CHAPTER VIII.

### GASTRIC DIGESTION.

THE stomach is a muscular membranous sac whose walls have, on an average, a thickness of a little more than a line. When distended, it measures laterally from thirteen to fifteen inches, and antero-posteriorly five inches, with a capacity, according to Brinton,<sup>1</sup> of one hundred and seventy-five inches, or about five pints. The capacity of the stomach, however, is often less and sometimes even much greater, varying with the age, sex, and habit of the individual. It is held in position in the upper part of the abdominal cavity by its connection with the œsophagus and the folds of the peritoneum. When empty, the sides of the stomach are usually in contact, and the whole organ presents a flattened appearance. When distended by food, however, the anterior wall of the stomach becomes superior, and is applied to the diaphragm. This is due to the ends of the stomach and lesser curvature being comparatively immovable. As the food enters the stomach from the œsophagus, it turns to the left, and, passing into the cardiac end, or greater pouch, thence proceeds along the greater curvature to the pyloric end, returning by the lesser curvature to the cardiac portion, to begin the same course over again. Each of these revolutions occupies from about one to three minutes; <sup>they</sup> ~~and~~ are slowest at first, becoming more rapid as digestion advances. The food undergoes, therefore, a sort of churning action, passing from one side of the stomach to the other. As the circular muscular fibres surrounding the pyloric orifice offer a resistance to solid undigested matter, it is only the liquid, pultaceous, digested food which escapes into the duodenum. After a time, however, even hard foreign bodies, like stones, coins, etc., make their way into the small intestine.

An interesting fact connected with the movements of the stomach, is a noticeable difference between the contraction of the pyloric as compared with that of the cardiac end of the stomach. The food while in the cardiac end of the stomach appears to be subjected to a simple pressure, whereas the action of the pyloric portion is of a vigorous expulsive character. Indeed, when digestion is at its height the cardiac portion of the stomach is quite distinctly separated from the pyloric portion by a constricting band. The organ then presents an hour-glass form, of which two-fifths consist of the cardiac portion. It is worth mentioning in this connection, that this hour-glass form of the stomach, present only in man during digestion, is the form presented in the manatee (Fig. 46) whether digestion is going on or not; the author<sup>2</sup>

<sup>1</sup> Cyclopædia of Anatomy and Physiology. Supplement, p. 308. London, 1837-1847.

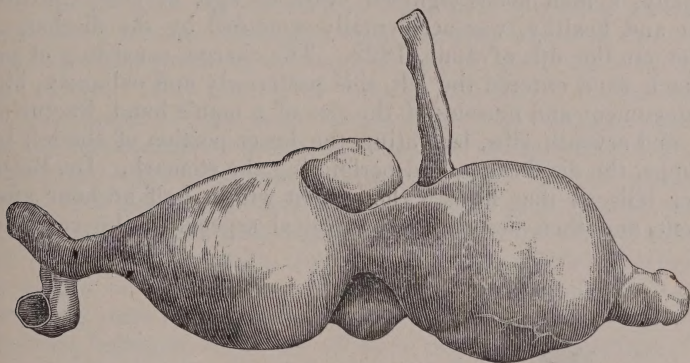
<sup>2</sup> Proceedings of Academy of Natural Sciences, Philadelphia, 1876, p. 452.



having found in the dissection of several individuals the stomach always presenting this form, whether it was full of food or empty.

After the food has been digested and the stomach has been emptied of its contents, which processes are effected within a period of from two to four hours, all the motions just described cease, and do not recommence ~~again~~ until a fresh supply of food is taken. The peristaltic

FIG. 46.



Stomach of manatee.

vermicular motion of the stomach that I have endeavored to describe, depends upon its muscular fibres, assisted by the diaphragm. The muscular coat of the stomach, which averages about the  $\frac{1}{4}$ th of an inch in thickness, consists of three sets of fibres, the longitudinal, circular, and oblique, which are disposed from without inward, in the order just named—that is, the longitudinal fibres are external, the oblique are internal, while the circular fibres lie between the other two.

These three sets of fibres are, however, very unequally developed. Thus, the longitudinal fibres are best seen in the lesser curvature; the circular fibres are rather indistinct to the left of the cardiac orifice, and are most marked at the pyloric, forming then its sphincter muscle; while the oblique fibres are limited to the cardiac portion of the stomach, passing over it from left to right. It is at the point where these oblique fibres cease that the stomach becomes constricted in digestion into the two parts already described.

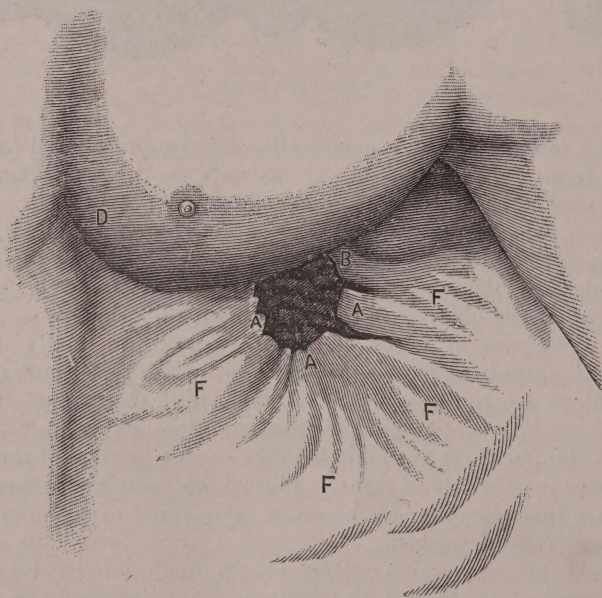
Through the contraction of the longitudinal and circular fibres the food is forced along toward the pylorus, which, through its sphincter muscle, resists at first all but thoroughly digested food. The cardiac orifice is guarded by the fibres in that situation, as well as by the contraction of the lower part of the œsophagus already referred to. The movement of the food is also due, no doubt, partly to the pressure exerted by the diaphragm and the intestines. The natural stimulus to these motions of the stomach during digestion is the presence of food. The account that we have just given of the movements that the stomach undergoes during digestion in man, is taken entirely from the experi-

ments and observations of Beaumont,<sup>1</sup> to whom physiology is so greatly indebted for much that is positively known of the human gastric digestion.

As what I have to say of the secretion of the gastric juice and its effect upon food in the living human body is, to a great extent, derived entirely from that classical work, it appears to me proper that I should narrate the main facts of the truly celebrated case which afforded Beaumont the opportunity of making his experiments and observations.

Alexis St. Martin,<sup>2</sup> a voyageur in the service of the American Fur Company, a man about eighteen years of age, of good constitution, robust and healthy, was accidentally wounded by the discharge of a musket on the 6th of June, 1822. The charge, consisting of powder and duck shot, entered the left side posteriorly and obliquely, blowing off integument and muscles of the size of a man's hand, fracturing the sixth and seventh ribs, lacerating the lower portion of the left lobe of the lungs, the diaphragm, and perforating the stomach. Dr. Beaumont further tells us that he saw the patient within half an hour after the accident, and then describes the surgical aspects of the case and the

FIG. 47.



Ordinary appearance of the left breast and side, the aperture filled with the valve ; the subject in an erect position. (BEAUMONT.)

treatment, and the gradual but perfect recovery of his patient so far as the general health was concerned. The perforation through the walls of the stomach, however, remained permanently open, having resisted all treatment. This perforation (Fig. 47) was situated three inches to

<sup>1</sup> Experiments and Observations on the Gastric Juice, pp. 96, 97, 110, 111, 113. Plattsburgh, 1833.

<sup>2</sup> Beaumont, *op. cit.* Introduction.



the left of the cardiac portion of the stomach, near the superior termination of the great curvature, and measured about two and a half inches in circumference. The opening was closed under ordinary circumstances by a movable valve formed through a doubling of the coats of the stomach, which had been formed during the progress of the case, and which effectually prevented the escape of food. This valve could be easily depressed, when the interior of the stomach could then be examined.

St. Martin, after the recovery of his health, performed all the duties of a common servant—chopping wood, carrying burthens, etc.—married and had several children, and enjoyed general good health up to eighty years of age. For a number of years, off and on, St. Martin was under the observation of Beaumont, under strictly physiological conditions. It is this circumstance which makes this case so important in the history of the physiology of digestion. There have been cases of gastric fistula in man, both before and since that of St. Martin, but either such cases were complicated with pathological conditions or the circumstances were such as to make constant, detailed, and trustworthy observation for any length of time, such as that given by Beaumont, impossible. Interesting cases of gastric fistula, the result of wounds or gastrotomy, have been, however, made use of more recently for purposes of physiological investigation, by Schmidt<sup>1</sup> and Richet,<sup>2</sup> and which will be referred to again.

In order to appreciate the immense value of this case of St. Martin, it should be mentioned that little was positively known of gastric digestion, as it takes place in man, before the observations and experiments of Beaumont were made.

Up to the middle of the eighteenth century it was still a subject of discussion whether the action of the stomach in digestion was of a chemical or mechanical nature. Among those who favored the chemical theory there were some who adhered to the view of the ancients, who considered that digestion consisted in a kind of cooking, while others held that the action was like that of putrefaction, or again of fermentation. On the other hand, of those who advocated the mechanical theory of digestion, some exaggerated greatly the triturating force of the walls of the stomach, while to others even holding this view objections had presented themselves, like that of the walls of the stomach being too thin in many animals to exercise any great mechanical force; while in birds, like the ostrich, in which, though the walls of the muscular gizzard are extremely thick and very powerful, digestion was still known to have taken place even when the walls of the stomach had been completely separated by a foreign body, like an impacted nail, and which prevented entirely any triturating action, as in the case mentioned by Valisneri, and referred to by Milne Edwards.<sup>3</sup> In this connection it may be mentioned that in dissecting an ostrich the author also found the walls of the stomach completely separated, the impacted body in that case being a piece of hard wood.

<sup>1</sup> Liebig's Annalen, 1854, xcii. S. 42.

<sup>2</sup> Comptes Rendus, tome lxxxiv. p. 450. Paris, 1877.

<sup>3</sup> Physiologie, tome cinquieme, p. 526.

The controversy between physiologists about the chemical and mechanical nature of digestion was brought to a termination by the discovery of Reaumur,<sup>1</sup> in 1752, of the existence of a gastric juice in birds, and of the demonstration that substances were softened and partly digested in the stomach of those animals, apart from any mechanical action of its walls. Familiar with the fact that birds of prey frequently vomit up their food, and that falconers were in the habit of making their birds vomit, they considering such action to be salutary in its effects; it occurred to Reaumur to take advantage of this circumstance with reference to examining the contents of the stomach during digestion.

After showing the triturating effect of the muscular gizzard in those birds in which it is much developed, he proceeded to experiment with birds in which the gizzard is little developed, like a buzzard, for example, in the following manner: Meat was placed in a tin tube, the openings at both ends being covered with a grating which would allow any fluid to pass into the tube and mix with the meat, while the meat would be unaffected by the mechanical action of the walls of the stomach, the walls of the tin tube being sufficiently strong to resist the latter. Having forced the tube into the stomach of a buzzard, several hours afterward the meat was found softened and partly digested. In substituting for the tube with the meat small pieces of sponge, Reaumur was able to collect, by pressing the sponges after they had been rejected, a small quantity of a liquid which gave an acid reaction, and which was the first specimen of a solvent fluid from the stomach ever obtained. Reaumur also performed some experiments with the gastric juice so obtained, but they were not satisfactory. In extending his experiments on birds, to dogs and sheep, Reaumur got pretty much the same results, and concluded<sup>2</sup> that meat can be digested in the stomach, not only without having been ground up, but without even having suffered the slightest rubbing. This operation can then be only the work of a dissolvent, of which the existence is well demonstrated. The next step in advance was made in 1777, by Edward Stevens, good use being made of a man who for years had been accustomed to exhibit his habit of swallowing stones. Stevens tells us in his *De Alimentorum Concoctione*,<sup>3</sup> that he used a hollow silver ball, perforated with numerous holes, and divided into two parts by a septum. In one compartment, for example, meat was placed, in the other bleak. The man would then swallow the silver ball. After twenty to forty hours it would be passed by the anus, and its contents would be found partially digested. Stevens experimented in this way with different kinds of food, and unless the food was very hard, the silver ball was usually found empty when passed by the anus, showing that some solvent must have passed into the ball. The individual, however, leaving Edinburgh, where the observations had been made, Stevens repeated his experiments upon dogs, making use of ivory balls, which were filled with different kinds of food, and obtained essentially the same results.

In summing up, Stevens concludes that his experiments prove clearly

<sup>1</sup> Memoires de l'Academie des Sciences, 1752, tome lxi. p. 461.

<sup>2</sup> Op. cit., p. 471.

<sup>3</sup> Thesaurus Medicus, Smellie Tomus iii, p. 481.



and manifestly that digestion cannot be accounted for by heat, trituration, putrefaction, or even fermentation alone, but by a most powerful humor which is secreted by the tunic of the stomach and is poured into the cavity of the same.

A few years later there appeared the celebrated work of Spallanzani, in which the observations of Reaumur and Stevens were repeated and confirmed, and extended in a series of experiments made upon quite a number and variety of animals, including several interesting observations made by the author upon himself, some of which have already been alluded to in speaking of the subject of mastication. Spallanzani<sup>1</sup> began his experiments upon himself by first swallowing little linen bags in which the different articles of food, animal or vegetable, were sewn up. These were usually passed by the anus within a period varying from twenty-three to twenty-four hours, and were found either empty or nearly so, the contents being more or less digested, according to the kind of food used and the length of time during which they had remained within the body. Emboldened by his success, Spallanzani tells us he ventured then to swallow little wooden tubes five lines in length and three in diameter, the sides of which were perforated with numerous little holes to permit the free ingress of the juices of the stomach. These tubes when passed by the anus, though very fragile, were never broken or bruised, which they would have been had they been subjected to a triturating action, while the meat which they contained being digested when passed by the anus showed that the result must be due to the solvent action of the gastric juice entering the tubes. The necessity of first masticating the food before swallowing it was then demonstrated; and, in conclusion, a little gastric juice was obtained by vomiting, and the effect of this upon boiled beef tried outside the body, with the result of showing that the beef became pulvaceous, and that there was no putrefaction. Spallanzani distinctly recognized a most important fact, that the process of digestion, beginning in the stomach, is completed in the intestines.

In 1824 Prout<sup>2</sup> endeavored to show, by analysis, that the acidity of the gastric juice in animals was due to hydrochloric acid.

Shortly afterward, between 1825 and 1827 simultaneously, Leuret and Lassaigue,<sup>3</sup> Tiedemann and Gmelin,<sup>4</sup> made a detailed and extended series of observations upon digestion; those of the latter being the most elaborate. The experiments were made principally upon dogs, cats, horses, cows, sheep, birds, reptiles, and fishes, the observations on man being exceptional. In some of the experiments the means of obtaining the gastric juice were the same as those used by Reaumur, etc., already referred to. In many of them, however, another plan was adopted. The animal to be experimented upon after fasting, was made to swallow stones, nails, etc., a few hours afterward the animal was killed, it having been ascertained that such hard substances would excite the stomach to secrete a considerable amount of gastric juice—sufficient in quantity to

<sup>1</sup> *Fisica Animale e Vegetabile*, tomo secundo, pp. 42, 41, 51, 52, 58, 64. Venezia, 1782.

<sup>2</sup> *Philosophical Transactions*, 1824.

<sup>3</sup> *Recherches pour servir à l'Histoire de la Digestion*. Paris, 1825.

<sup>4</sup> *Recherches sur la Digestion*. Paris, 1837.

analyze and to experiment with. Notwithstanding the number and variety of the animals experimented upon by these physiologists, their conclusions were not entirely satisfactory, as the results of their experiments and observations were often contradictory and inconsistent. While the composition and properties of the gastric juice were, to a certain extent, known, great difference of opinion still prevailed as to what elements it owed its digestive powers, and exactly what effect it had upon different kinds of food. Further, while many observations were made, and some definite conclusions drawn as regards digestion in animals, little or nothing was added by Prout, Leuret and Lassaigne, Tiedemann and Gmelin to the knowledge of digestion as it takes place in man, already gained from the experiments of Stevens and Spallanzani.

Leaving this little historical digression, which was indispensable in order to appreciate the value of the observations of Beaumont, let us see now what was established by this physiologist.

Beaumont was the first to observe digestion as it goes on in the healthy human stomach, to describe not only the motion of the latter, but also the manner in which the gastric juice is secreted, its effect upon food, the changes that food undergoes in the stomach, to collect the normal gastric juice in such quantities that it could be analyzed and studied with reference to its effect upon food outside the body. Indeed, it is not too much to say that with the exception of Schmidt's case in Dorpat, and Richet's in Paris, to be mentioned again shortly, all that is positively known of gastric digestion in man is derived from the case of St. Martin. I mention this particularly, as there seems to be a widespread impression that our knowledge of gastric digestion in man is derived entirely from gastric fistula made upon dogs, it being taken for granted that the dog can be compared with man in this respect, the fact of the animal being a carnivorous one being altogether lost sight of. Curiously enough, it is also often forgotten that it was the case of St. Martin that suggested to Bassow,<sup>1</sup> the Russian naturalist, the experiment of making a gastric fistula upon a dog. It may be mentioned in this connection that Blondlot<sup>2</sup> usually gets the credit of having done this first, no doubt from his having popularized this very important experiment, and from his numerous observations on digestion. The manner of performing this operation, which is sufficiently simple, consists<sup>3</sup> essentially, a dog being used, in making an incision about two inches long in the median line into the abdominal cavity, beginning at about one inch below the ensiform cartilage. The stomach is then drawn out of the abdominal cavity, and a slit just large enough to admit the canula is made parallel with the longitudinal fibres. The canula, preferably of silver, about two inches long, and half an inch in diameter, is provided at both ends with a rim or flange, by which it can be securely ligated to the edge of the opening in the stomach and the opening in the abdominal walls. The wound cicatrizing around the canula, a permanent fistula into the stomach is established. The animal in a short time

<sup>1</sup> Bulletin de la Société des Naturalistes de Moscow, 1843, tome xvi. p. 315.

<sup>2</sup> Traité analytique de la digestion, 1843.

<sup>3</sup> Bernard: Physiologie Experimentale, tome ii. p. 384. Paris, 1856.



suffers no inconvenience whatever, and will serve indefinitely as a means of obtaining natural gastric juice.

In order to study digestion in man it is not necessary, however, to make a gastric fistula in a dog, as Eberle<sup>1</sup> showed in 1834, that if the mucous membrane of the stomach be macerated in water slightly acidulated a liquid is obtained which will act upon food in the same manner as the natural gastric juice, and which is, in fact, an artificial gastric juice. Eberle fell into the error, however, of supposing that he could obtain the same results from an acidulated infusion made of any mucous membrane whatever.

It may be mentioned in this connection that, as the opportunity does not always present itself of obtaining the mucous membrane of the human stomach in a perfectly fresh condition, that of the pig will do equally well, as shown by Kolliker<sup>2</sup> and others, which is perfectly intelligible when it is remembered that its mucous membrane is almost identical with that of man. Before describing the phenomena of digestion in man, as learned from the observations of Beaumont, Schmidt, Richet, and experiments with artificial gastric juice, let us first consider the structure of the mucous membrane of the stomach which secretes the juice, through which digestion in this part of the alimentary canal is effected.

The mucous membrane of the stomach, in the living healthy subject, is of a velvety, pulpy consistence, with an average thickness of about the  $\frac{1}{20}$ th of an inch, and in color of a pale pink or reddish appearance, which rapidly changes after death into a brownish hue. The mucous membrane is loosely attached to the submucous coat or the layer of areolar tissue which lies between the mucous coat within and the muscular coat without. It is through the looseness of this attachment that the longitudinal folds into which the membrane is usually thrown are due, and which are effaced when the stomach is distended. The epithelium covering the mucous membrane of the stomach is of the columnar character, and presents more particularly at the cardiac orifice, a marked contrast as compared with the pavement epithelium lining the œsophagus.

If the mucous membrane of the stomach be gently washed by allowing a small stream of water to run over it slowly, which will carry off the adhering mucus, and then be examined with a simple lens, little polygonal spaces or depressions will be noticed in its surface, varying in size from the  $\frac{1}{100}$ th to the  $\frac{1}{200}$ th of an inch in diameter. If these depressions or alveoli be further examined with the microscope, they will be seen to consist of a number of small round apertures of about the  $\frac{1}{350}$ th to  $\frac{1}{500}$ th of an inch in diameter. These minute apertures are the mouth-like openings of the gastric follicles, small tubules varying in length from the  $\frac{1}{20}$ th to the  $\frac{1}{60}$ th of an inch, and which are imbedded in the mucous membrane, the blind or closed ends of the tubules looking outwardly toward the submucous coat, the open ends inwardly toward the interior of the stomach (Fig. 48).

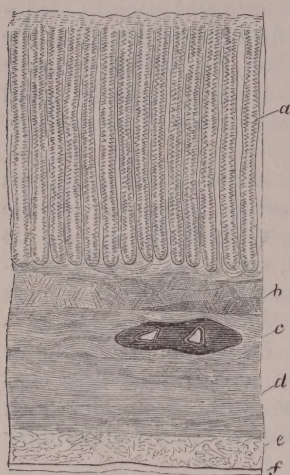
The gastric tubules of the ostrich, or the water-cells of the first

<sup>1</sup> Physiologie der Verdauung, S. 80. Würzburg, 1834.

<sup>2</sup> Gewebelehre, Funfte Auflage, S. 402.

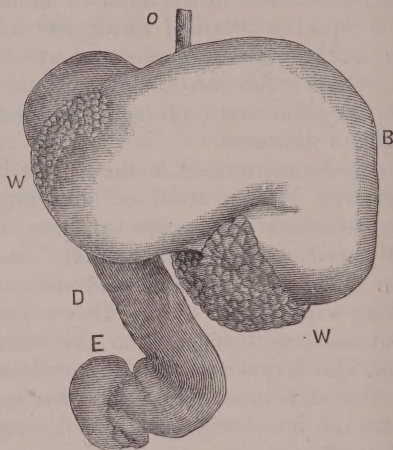
stomach of the llama (Fig. 49) give an excellent idea of the general disposition of the gastric glands of the human stomach. It need hardly

FIG. 48.



Vertical transverse section of the coats of a pig's stomach. 30 diameters. *a.* Gastric glands. *b.* Muscular layer of the mucous membrane. *c.* Submucous or areolar coat. *d.* Circular muscular layer. *e.* Longitudinal muscular layer. *f.* Serous coat. (After KOLLIKER.)

FIG. 49.



Stomach of llama. Water cells seen from outside.

be mentioned that the water-cells of the llama do not contain gastric juice, the latter being secreted by the tubules of the fourth stomach. The gastric tubules differ considerably in their structure and form, according to the part of the stomach examined.

Thus, in the pyloric portion of the stomach the tubules (Fig. 50) are lined, to a certain extent at least, with a continuation of the columnar epithelium covering the inner surface of the stomach; in the upper parts, however, of these tubules the lining cells become shorter and more cubical in character, and correspond according to Ebstein<sup>1</sup> and Heidenhain<sup>2</sup> in their function with the central cells found in the tubules found in the cardiac part of the stomach. The pyloric tubules, while terminating usually in a branched manner, terminate also simply. If the middle zone of the stomach be now examined, both simple (Fig. 51) and branched tubules (Fig. 52) will be found resembling those in the pyloric portion, but while the upper portion of the tubule (Figs. 50, 51) is lined with columnar epithelium, the succeeding part or neck is filled rather than lined by large ovoidal or spheroidal granular cells of about the  $\frac{1}{1200}$ th of an inch in diameter, the so-called ovoid cells, formerly, however, known as peptic cells. Toward the bottom or fundus of the gland these peptic or ovoid cells (Fig. 51, P) do not form a continuous layer, but are seen scattered here and there, and bulging out so as to give the tubule a varicose appearance, the remaining portion of the tubule, except the narrow passage-way in the middle, being occupied by

<sup>1</sup> Archiv f. Mic. Anat., Band vi. S. 515, 1870.

<sup>2</sup> Hermann: Physiologie, Funfter Band, S. 598. Leipzig, 1880.

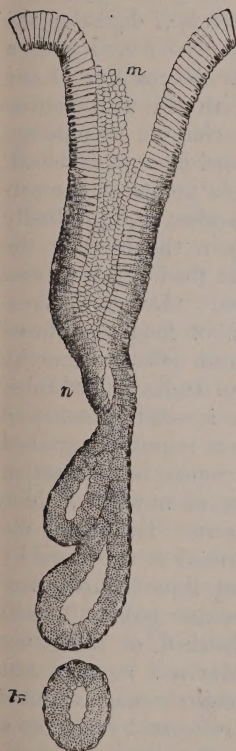


finely granular polyhedral angular cells, the so-called central cells, similar, as just mentioned, to those found in the pyloric tubules. In the cardiac portion of the stomach, more particularly around the cardiac orifice, the tubules are branched in character, the upper part of the

tubule dividing into two or three branches, and there usually subdividing again. These cardiac tubules, like simple ones found in the middle zone of the stomach, contain both ovoid and central cells. It will be observed from this brief description that two kinds of glands are found in the human and canine stomach, differing essentially in their structure:

FIG. 50.

M

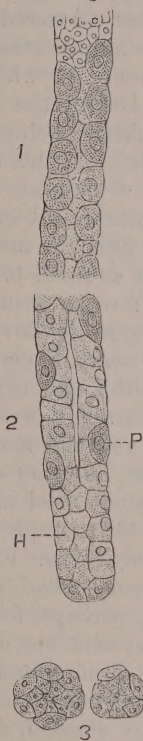


75

Gastric glands from the dog's stomach. M. A pyloric or mucous gland. m. Mouth. n. Neck. tr. A deep portion cut transversely. (After EBSTEIN.)

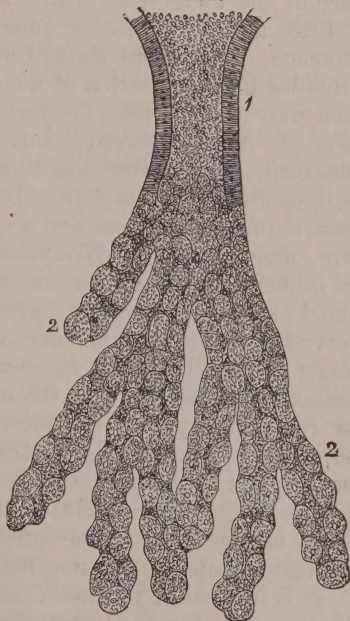
FIG. 51.

C



Gastric glands from the dog's stomach, highly magnified. 1. Neck of the gland. 2. Fundus. 3. Transverse section. P. Peptic or ovoid cells. H. Central cells. C. Ends of columnar cells. (After HEIDENHAIN.)

FIG. 52.



Gastric gland from human stomach. 1. Columnar cells. 2. Ovoid cells. (KOLLIKER.)

pyloric tubules, simple and branched, situated in the pyloric part of the stomach, containing columnar, epithelial, and central cells; cardiac tubules, simple and branched, situated in the middle and cardiac parts of the stomach, containing columnar, epithelial, and central cells, and ovoid cells also.

While undoubtedly such a distinction as that just described exists between the gastric glands in man, the exact line of demarcation is not as distinct as in that of the dog; the different kindsof glands passing in /s

man into each other through intermediate forms. Around the cæcal ends of the cardiac tubules, more particularly, are usually found a few involuntary muscular fibres, the effect of the contraction of which is to force out their contents. The stomach is a highly vascular organ, as one would suppose from the large size of the arteries supplying it. It is not necessary, however, to describe in detail its vascular supply, and simply mentioning, also, that at the pyloric portion of the stomach some rudimentary villi are found, and that scattered all through the organ solitary glands may be seen, whose minute structure will be considered elsewhere, I will pass on to the manner in which the gastric juice was said to be secreted in St. Martin. During the intervals of digestion the stomach is empty, its mucous membrane being simply covered with a very thin, transparent, viscid mucus. At this time the reaction of the membrane is either faintly alkaline or neutral. With the introduction of food into the stomach, the membrane at once changes its pale appearance, becoming red and turgid from the increased amount of blood. Small drops of gastric juice appear as small pellucid points on the surface of the membrane, which has now an acid reaction, and gradually a little stream of gastric juice begins to flow upon the food in the stomach. Beaumont showed most conclusively that food is the natural stimulus to the secretion of the healthy gastric juice. "Let good digestion wait on appetite," for the exciting impression of food is diffused over the whole secreting surface, and the maximum effect is thereby obtained. Local stimulus, however, like that of an India-rubber tube, will excite a flow, and this Beaumont used when a small quantity of gastric juice—an ounce and a half, for example—was required unmixed with mucus or food. Everyone knows from experience, how digestion is influenced by the nervous system—a bad piece of news, a sudden shock, stopping digestion entirely, perhaps, for hours. Beaumont observed that whenever the nervous system was disturbed or depressed by anger or fear, by undue excitement from stimulating liquors, from overloading the stomach, etc., the mucous membrane became pale and moist or red and dry, and the secretions vitiated, diminished, or altogether suppressed. It was also noticed that when St. Martin's stomach was out of order or inflamed, the same kind of morbid condition was exhibited by the tongue, the condition of the latter being relieved by placing a little magnesia upon the surface of the stomach, thus illustrating the intimate sympathy existing between the two organs.<sup>1</sup>

It is impossible to state exactly the amount of gastric juice secreted by a man during the twenty-four hours. Approximately it may be said to amount to about seven kilogrammes (fourteen pounds) daily. This estimate is based upon the amount of gastric juice absolutely collected from animals whose weight was compared with that of an adult man,<sup>2</sup> and by the amount of gastric juice necessary to digest a known quantity of meat, one gramme of meat (about half a drachm) requiring 13.5 grammes (about one fluidounce) of gastric juice.<sup>3</sup> It must be remembered, however, that the gastric juice is being reabsorbed with the food

<sup>1</sup> Beaumont, *op. cit.*, pp. 103, 104, 105, 106, 107, 108, 109.

<sup>2</sup> Schmidt: *Liebig's Annalen*, 1854, xcii. S. 46.

<sup>3</sup> Dalton's *Physiology*, 7th ed., 1882, p. 162.



as it is being secreted, and that, therefore, there is some risk of counting the same gastric juice, or the elements of the same, over again. Observations made upon dogs by Blondlot,<sup>1</sup> may be mentioned here in reference to the influence that swallowing food has upon the amount of the gastric juice secreted. This experimenter noticed that alkalies increase the flow of the gastric juice while acids diminish it, hence the importance of the alkaline saliva in promoting gastric digestion. But the mere effect of gustation, apart from the admixture of the saliva with the food, exerts an influence on the flow of the gastric juice, for when sugar, even when mixed with saliva, was passed directly into the stomach of the dog through the fistulous opening, a smaller quantity of gastric juice was secreted than when the sugar was first introduced through the mouth. The experiments of Kolliker,<sup>2</sup> Goll, and Donders with the mucous membrane of the stomach of man and the pig, and which the author has had opportunities of confirming, show pretty conclusively that the true gastric juice is only secreted by the cardiac tubules, or those tubules which contain both ovoid and central cells; the pyloric tubules, containing only central cells, supplying probably pepsin; the columnar epithelial cells lining the interior of the stomach and more or less prolonged into the cardiac and pyloric tubules, elaborating mucus.

Judging from what has been learned of the process of salivary secretion, analogy would lead us to suppose that the gastric juice is secreted in an essentially similar manner, and such would appear to be the case, as shown more particularly by the researches of Heidenhain.<sup>3</sup> Thus, if sections of the gastric glands of an animal be examined before the taking of food, the so-called central cells of the cardiac, as well as those of the pyloric glands, will be found pale, finely granular, and not staining readily with aniline or carmine. With the beginning of digestion, however, these cells become swollen, coarsely granular, turbid, and stain more readily with the above reagents; as digestion continues, the coarse, granular, and turbid condition and disposition to stain increase, while at the same time the cells become smaller and shrunken. The only conclusion to be drawn from the changes in the character of these cells is, that the development of a coarsely granular, readily stainable material, etc., during digestion constitutes the elaboration out of that albuminous principle of the gastric blood of either pepsin itself, or, what is more probable, of pepsinogen, or a stage in the formation of the same—a propepsin, so to speak. And since the changes just described take place equally in the centre cells of the pyloric, as well as of the cardiac portion of the stomach, it follows, as held by Heidenhain,<sup>4</sup> that the former as well as the latter produce pepsin, and this conclusion, based upon histological grounds, is confirmed by the physiological fact of an acid infusion of the pyloric glands possessing digestive properties. Inasmuch, however, as the ovoid or peptic cells of the cardiac portion of the stomach do not exhibit during digestion the histological changes observed in the central cells of the cardiac and pyloric glands, only swelling up and projecting somewhat externally from the wall of the gland, and from the fact of ovoid cells being present

<sup>1</sup> Op. cit., p. 219.

<sup>3</sup> Hermann: Handbuch, Funfter Band, 1880, S. 141.

<sup>2</sup> Loc. cit.

<sup>4</sup> Ibid., S. 130.

in the glands of the stomach of the frog coincidently with the presence of acid, the pepsin-forming cells being confined almost entirely to the lower part of the œsophagus in that animal, it would seem reasonable to attribute, with Heidenhain,<sup>1</sup> to the ovoid cells the production of the acid of the gastric juice, either out of the sodium chloride of the blood, or some less stable chloride compound. If such be the case, however, it is somewhat difficult to understand why, after injecting ferrocyanide of potassium and ferric lactate into the blood of an animal, as in the experiment of Bernard,<sup>2</sup> the production of Prussian blue should be limited to the surface of the stomach, since if the ovoid cells of the glands actually produce the acid the presence of which is necessary for the formation of the salt, the Prussian blue should be visible in the cells of the fundus or their vicinity, as well as upon the surface or mouth of the gland, unless the acid is expelled from the gland as rapidly as produced, which is not improbable.

It may be mentioned in this connection, that the acidity of the long, tubular-like gastric glands of birds is also restricted to the mouths of the glands.

Notwithstanding what has just been said, it must be admitted that the physico-chemical changes upon which the elaboration of the gastric juice depends, are, as regards many points, still very obscure.

<sup>1</sup> Op. cit., S. 135, 148.

<sup>2</sup> *Liquides de l'Organisme*, tome ii. p. 375. Paris, 1859.



## CHAPTER IX.

### GASTRIC DIGESTION.—(*Continued.*)

#### COMPOSITION OF GASTRIC JUICE.

THE first to attempt to analyze the gastric juice was Scopoli, an Italian chemist, in the last century. The gastric juice examined was obtained by Spallanzani from a raven, and, according to Scopoli,<sup>1</sup> consisted of an animal matter, earthy salts, and what would now be called hydrochloric acid. The gastric juice of St. Martin was examined by the late Professor Dunglison, who, in a letter to Beaumont,<sup>2</sup> states that it contained free muriatic and acetic acids, phosphates, and muriates, with bases of potassium, sodium, magnesium, and calcium, and an animal matter soluble in cold water, but insoluble in hot; the specific gravity, according to Silliman, being 1.005. Numerous analyses, during the early part of this century, were also made of the gastric juice of different kinds of animals by Prout, Leuret and Lassaigne, Tiedemann and Gmelin, and later by Bernard, and Barreswil,<sup>3</sup> Blondlot, and others. The results of these analyses essentially agree so far as relates to the presence of salts and an animal matter. The main difference in them is as regards the acid that gives the gastric juice its decidedly acid reaction. The most minute and thorough analysis of the human gastric juice yet made is that of Schmidt. Schmidt and his pupils had under observation for several weeks in Dorpat a woman who had a fistulous opening in the stomach, and, as her general health was good, there is no reason to suppose that her gastric juice was abnormal in any respect. Table XXXV. gives the mean of two distinct analyses made of the woman's juice by Schmidt:

TABLE XXXV.<sup>4</sup>—COMPOSITION OF HUMAN GASTRIC JUICE  
HOLDING SALIVA.

|                    |                       |                |
|--------------------|-----------------------|----------------|
| Water              | . . . . .             | 994.400        |
| Pepsin, etc.       | . . . . .             | 3.195          |
| Hydrochloric acid  | . . . . .             | 0.200          |
| Calcium chloride   | . . . . .             | 0.061          |
| Sodium chloride    | . . . . .             | 1.464          |
| Potassium chloride | . . . . .             | 0.550          |
| Calcium            | } phosphate . . . . . | 0.125          |
| Magnesium          |                       |                |
| Ferrum             |                       |                |
| Loss . . . . .     |                       | 0.005          |
|                    |                       | <hr/> 1000.000 |

<sup>1</sup> Spallanzani, op. cit.

<sup>3</sup> Comptes Rendus, 1844, tome ix.

<sup>2</sup> Op. cit., pp. 78, 81.

<sup>4</sup> Annalen der Chemie, 1854, Band xcii. S. 46.

Schmidt gives as the mean of the two analyses the number 994.404 for the water, and 1.465 for the sodium chloride. This is probably a typographical error, as the other numbers are those given in the table.

The loss, which is fractional in the mean of the two analyses, is not given in the original paper.

It will be seen from this analysis that human gastric juice consists of water, pepsin, hydrochloric acid, chlorides, and phosphates. Pepsin, the organic nitrogenized principle of the gastric juice, was discovered and named by Schwann,<sup>1</sup> though more thoroughly investigated by Wasmann. It is usually prepared at the present day by making an infusion of the stomach, filtering and precipitating by lead acetate; sulphuretted hydrogen being then added to the precipitate, an insoluble lead oxide is formed, and the pepsin is set free. This is further treated with absolute alcohol, and then appears as a whitish neutral powder. When pepsin is dissolved in slightly acidulated water an artificial gastric juice is obtained differing but little, except in power, from the natural secretion. The pepsin obtained directly from the gastric juice by treating with alcohol is more powerful than that derived by the methods just referred to. In the amount of pepsin given in Table XXXV. it should be mentioned that a small trace of ammonia was reckoned with it, which was probably developed during the analysis. At the present day there is still some question among physiologists as to whether the acidity of the gastric juice in animals depends upon hydrochloric or lactic acid.

What interests us at this moment is as to the acidity of the human gastric juice. It has been ascertained that it is immaterial whether the pepsin be acidulated with hydrochloric or lactic acid so far as its digestive action is concerned, the only difference being that a greater effect is obtained with the hydrochloric than with the lactic acid: *à priori*, then we might expect to find either acid, or even both, according to the circumstances under which the individual is living whose gastric juice is analyzed. As a matter of fact, free hydrochloric acid was obtained with great readiness by the late Professor Dunglison from the gastric juice of St. Martin, and, as we see from Table XXXV., by Schmidt, from that of the woman in Dorpat. The objection is often made that the hydrochloric acid obtained by these observers was due to their method of analysis: its presence being due to the lactic acid decomposing the alkaline chlorides at a certain elevation of temperature, it being assumed that lactic acid is the free acid of the gastric juice. On the other hand, it is well known that under certain conditions lactic acid is generated in the system in the secretions or from the food, and its presence in the gastric juice may, therefore, at times be accidental. It is proper to state, however, that the late Prof. F. G. Smith,<sup>2</sup> in examining the gastric juice of St. Martin, in 1856, found mostly free lactic acid, but little hydrochloric. An important observation, bearing upon this question, was made by Prof. Graham.<sup>3</sup> Some fluid, supposed to be gastric juice, obtained by the late Dr. Bence Jones

<sup>1</sup> Muller's Archiv, 1836, S. 66.

<sup>2</sup> Philadelphia Examiner, Philadelphia, 1856, p. 393

<sup>3</sup> Carpenter's Physiology, 8th ed., p. 156.



from a patient affected with *sarcina ventriculi*, was analyzed by the method of dialysis, which does not involve heat, and gave signs of containing both hydrochloric and lactic acids, the latter being comparatively small in quantity.

The question of the acidity of the human gastric juice reduces itself, therefore, as to whether it depends upon hydrochloric or lactic acid, or both. The evidence at present seems to us to favor the view that hydrochloric acid is the acid of the gastric juice. Practically, however, so far as digestion is concerned, either of these acids, or even acetic will do, though it is not true that any acid will replace the hydrochloric or lactic; acids, like malic, tartaric, tannic, etc., retarding or stopping digestion. The most important fact in gastric digestion is that the pepsin should be acidulated with either hydrochloric or lactic acid. Pepsin without acid will not digest, and, on the other hand, acidulated water without pepsin is equally without digestive effect.

Whether the acid and the pepsin are united in the gastric juice, acting as one substance, or whether they exist there independently, has not yet been positively determined. The remaining matters entering into the composition of the gastric juice are unessential in digestion, so far as is at present known.

Let us now turn to a consideration of the action of the gastric juice upon the different articles of food. Our knowledge in this respect, so far as the living man is concerned, is essentially based upon the observations of Beaumont,<sup>1</sup> supplemented by those of Schmidt, Richet, etc. The principal effects of the gastric juice upon food, as observed in man, can, however, be easily demonstrated with a gastric juice artificially prepared in the following manner:

The dried mucous membrane of the stomach is cut up into small pieces and placed in suitable test-tubes, into which distilled water is then poured. To this infusion of the mucous membrane there should then be added a few drops of hydrochloric acid. The artificial gastric juice so prepared should further be maintained at a temperature of about 100° F. Into the test-tubes can now be put small pieces of coagulated white of egg, boiled meat, etc., and which, when left there about twelve hours, will be found digested. A little stirring from time to time will aid the process.

In order to show the necessity of the combined effects of the pepsin and the acid, it is well to have at the same time one test-tube containing the macerated mucous membrane only, and another with acid, but without the prepared membrane. The food in these two test-tubes will be found comparatively unchanged, that in the tube containing the hydrochloric acid having become only syntonin. Post-mortem examinations made upon individuals dying during digestion also offer opportunities of examining the effect of the gastric juice upon food, which, unfortunately, are too often neglected. At one time it was supposed that the gastric juice acted upon all kinds of food. It is well known now, however, that its action is limited almost entirely to those foods containing nitrogenized principles, such as meat, milk, eggs, gelatin, cheese, bread and other

<sup>1</sup> Op. cit., pp. 125, 126, 127, 148, 149, 200.

vegetable foods containing gluten; the starches, sugars, oils, and fats undergoing little if any change in the stomach. When meat is subjected to the action of the gastric juice, whether obtained from a fistula in the stomach or artificially prepared, it will be observed that it gradually becomes softer, changes in color, and breaks down into a grumous, pul-taceous mass. Under the microscope the muscular fibres, though broken up into small pieces and retaining but little tenacity, are readily recog-nized through their characteristic striæ. The intermuscular connective tissue, sarcolemma, has disappeared, however, being completely dis-solved out. Meat is, therefore, not actually dissolved in the stomach—it is rather disintegrated into a pultaceous liquid, which, passing easily into the small intestine, is there still further digested. Beaumont, in his experiments with natural gastric juice, usually used about one ounce of gastric juice to one drachm of food.<sup>1</sup>

It is a matter of common observation that raw or soft-boiled eggs are more easily digested than hard-boiled ones; and experiments, both with the natural and artificial juice, show that the raw white of egg is more quickly broken down, disintegrated, and the pure albumen separated from the membranous sacs, than when the cooked egg is used. Gelatin is rapidly dissolved by the gastric juice; and casein, as in milk, is first coagulated by it and then digested like coagulated albumen. The gastric juice not only acts physically upon the nitrogenized articles of the food, softening, disintegrating them, etc., but so changes the molecular ar-rangement of the chemical principles composing them that they cannot be recognized by the usual tests for albumen, such as heat, nitric acid, etc.

Thus albumen becomes albuminose or albumen-peptone, differing from albumen also in one most important respect—that it can be ab-sorbed, whereas albumen when injected undigested into the blood will be excreted by the kidneys, it not being assimilated.<sup>2</sup> Casein is changed during gastric digestion into casein-peptone, fibrin into fibrin-peptone, etc. Milk, as is well known to those engaged in the making of cheese, is curdled by the gastric juice—that is to say, its casein is precipitated. This effect is not due, however, as might be supposed, to the acid present, as gastric juice after being neutralized is still efficacious in this respect, but probably to some special ferment, since the neutralized gastric juice, after boiling, loses this property, and from the fact that the effect is largely dependent upon temperature. The general product of the digestion of the albuminous or nitrogenized principles by the gastric juice is often spoken of as albuminose or peptone, so named by Mialhe<sup>3</sup> and by Lehman,<sup>4</sup> respectively. The peptones all agree in being soluble in water and not precipitated by heat, acids, or alkalies, and eminently diffusible. As shown, however, by both these chemists, slight differences exist between these products of digestion, according to the particular kind of food used, and hence it is more proper to speak of them in the way just indicated.

Much difference of opinion still prevails among physiologists as to the changes which albuminous substances undergo during digestion.

<sup>1</sup> Op. cit., p. 269.

<sup>2</sup> Bernard: *Liquides de l'Organisme*, tome i. p. 467. Paris, 1859.

<sup>3</sup> *Memoire sur la digestion et l'assimilation des matieres albuminoides*. Paris, 1847.

<sup>4</sup> *Lehrbuch der physiologischen chemie*, Band ii. S. 46.



According to Brucke,<sup>1</sup> albuminous substances are converted in the stomach first into syntonin, and then into peptone, a simple expression of the facts we have just demonstrated, the phenomenon being essentially, according to Hoppe-Seyler,<sup>2</sup> one of hydration in the presence of pepsin. Meissner,<sup>3</sup> however, holds that albumen is only imperfectly digested by gastric juice, becoming peptone and parapeptone, the latter being an imperfect form of peptone, and requiring further digestion in pancreatic juice to convert it into peptones; while, according to Kuhne,<sup>4</sup> albuminous substances undergo still more complex changes in being transformed into peptone, the albumen being first converted into two substances, each of which passes through a series of intermediate stages before becoming what is called by Kuhne antipeptone and hemipeptone; the one series, to which the antipeptone belongs, being acted upon more particularly by the pepsin of the gastric juice; the other, to which the hemipeptone belongs, by the gastric and pancreatic juices combined; the hemipeptone, through the influence of the trypsin of the pancreatic juice, being finally converted into leucin, tyrosin, etc. Until, however, the facts upon which such views are based are better established and the contradictions involved are reconciled, it will be impossible to say which of the above views, if any, is entitled to the most credit as representing the actual changes through which albuminous substances pass in becoming peptones.

A curious fact during the action of the gastric juice upon meat, and not yet understood, is the absence of putrefaction. The explanation usually offered of this, that two catalytic actions do not go on simultaneously, is simply a restatement of the fact to be explained, catalysis being simply a convenient word expressing our ignorance of the phenomena. The action of the gastric juice upon fats appears to consist simply in dissolving the fat vesicles and so allowing the escape of their oily contents. When fat is taken into the stomach as oil it passes through the pylorus into the small intestine unchanged. Glucose or grape sugar does not appear to be affected by the gastric juice, and it is probable that this kind of sugar is at once absorbed as soon as taken into the stomach. Experiments with artificial gastric juice upon cane sugar show, however, that after several hours it is converted into grape sugar. This effect seems to depend simply on the acid of the gastric juice, and as the change takes place very slowly, it is not likely that any amount of cane sugar is converted into glucose in the stomach.

There is still some doubt as to the effect of gastric juice upon starch in the stomach. This is due to the fact that the saliva will continue to transform starch into sugar after the food has passed into the stomach, the gastric juice, in man at least, not interfering with this action. When starch is therefore transformed into sugar in the human stomach it is probably due to the saliva swallowed. It should be mentioned, however, that, according to the late Prof. F. G. Smith,<sup>5</sup> starch was converted into sugar when introduced directly into the stomach of St. Martin, though

<sup>1</sup> Vorlesungen, Erster Band, S. 311. Wien, 1881.

<sup>2</sup> Physiol. Chemie, II. Theil, S. 227. Berlin, 1878.

<sup>3</sup> Zeits. f. Rat. Med., vii. 1; viii. 280; x. 1; xii. 46; xiv. 303.

<sup>4</sup> Verhand. Nat. Hist. Verein. Heidelberg, 1876.

<sup>5</sup> Op. cit., p. 518.

the man carefully avoided swallowing his saliva during the period of the experiment. The effect in this case, however, was probably due not to the gastric juice, but to the gastric mucus.

Artificial gastric juice out of the body has no effect upon starch so far as the formation of sugar is concerned; it will, however, dissolve the cells and set free the starch when the substance is used in this form. It was shown by Beaumont that bones are, to a certain extent, digested by the gastric juice, a small portion being dissolved. As the calcium phosphate and carbonate are so indispensable in nutrition, and as the calcium biphosphate is soluble in acids, the stomach is that part of the alimentary canal where one would naturally look for the solution of bone in digestion.

According to Beaumont,<sup>1</sup> water, alcohol, and other fluids seem to be unaffected by the gastric juice, passing either into the intestine or being directly absorbed by the stomach.

In making experiments upon digestion with natural or artificial gastric juice, it will be found that in order to insure success a temperature of about 100° F. should be constantly maintained.

From a great number of experiments performed upon St. Martin, Beaumont<sup>2</sup> concluded that the natural temperature of the human stomach was 100° Fahr., and that the injection of food into the stomach did not elevate the temperature. The importance of heat in digestion will be seen when this function is contrasted in the hot- and cold-blooded animals; in the latter, where the heat of the body is about that of the surrounding air during winter digestion stops altogether, or goes on very slowly; while in the former, the temperature being independent of external conditions, at least within narrow limits, digestion goes on independent of change in the season.

In reference to the influence of exercise upon digestion, Beaumont<sup>3</sup> observed that moderate exercise conduces considerably to healthy and rapid digestion; severe and fatiguing exercise, on the contrary, retards it. This is readily understood when it is remembered that exercise elevates the temperature and accelerates the circulation. On the other hand, if too much blood is diverted from the stomach to the brain or extremities by much mental or physical exercise indigestion ensues. No rules, however, can be laid down absolutely in this respect. In some individuals there is an uncontrollable desire to sleep after eating, the good effects of which are so evident that it is absurd to resist the feeling, whereas, in other cases, gentle exercise is equally imperatively demanded.

It is a matter of common observation that animals, as a general rule, take little or no exercise after eating. That digestion is retarded, and even entirely stopped, by too much exercise, the author has had ample opportunities of observing from post-mortem examination made both on human beings and animals who had eaten food a short time before death, and who were known to have taken a considerable amount of, and often violent, exercise during that period. Other physiologists

<sup>1</sup> Op. cit., p. 97.

<sup>2</sup> Op. cit., pp. 273, 276.

<sup>3</sup> Ibid., p. 94.



seem to have had the same experience. Thus, in the last century, as related by Saunders,<sup>1</sup> Dr. Harwood, of Cambridge, procured two dogs, equally well fed; one of these he kept quiet, the other he compelled to take constant exercise immediately after eating. A few hours after feeding both dogs were killed. The food was found entirely digested in the stomach of the dog that had been kept quiet, while in that of the one that had been compelled to take the exercise the food was undigested.

TABLE XXXVI.<sup>2</sup>—DIGESTION OF FOOD IN STOMACH.

| Kind of food.                              | Time.           |
|--------------------------------------------|-----------------|
| Pig's feet, tripe . . . . .                | 1 hour.         |
| Salmon, trout . . . . .                    | 1 "             |
| Barley soup . . . . .                      | 1 hour 30 min.  |
| Milk . . . . .                             | 2 hours.        |
| Potatoes, roasted; beans, boiled . . . . . | 2 "             |
| Roast turkey . . . . .                     | 2 hours 30 min. |
| Soft boiled eggs . . . . .                 | 2 " 30 "        |
| Beefsteak, broiled . . . . .               | 2 " 30 "        |
| Pork, raw . . . . .                        | 3 hours.        |
| Hard boiled eggs . . . . .                 | 3 "             |
| Mutton soup . . . . .                      | 3 hours 30 min. |
| Oyster soup . . . . .                      | 3 " 30 "        |
| Potatoes, boiled . . . . .                 | 3 " 30 "        |
| Beef and vegetable soup . . . . .          | 3 " 30 "        |
| Duck, roasted . . . . .                    | 4 hours.        |
| Veal, broiled . . . . .                    | 4 "             |
| Veal, fried . . . . .                      | 4 "             |
| Pork, boiled . . . . .                     | 4 hours 30 min. |
| Cabbage, boiled . . . . .                  |                 |
| Pork, roasted . . . . .                    | 5 hours 15 min. |

It will be observed from Table XXXVI., taken from the much more extensive one of Beaumont, that certain articles of food are digested in the stomach much more rapidly than others. Thus, pig's feet, tripe, are digested in one hour, milk and roast potatoes in two, soft boiled eggs in three hours, hard boiled in three and a half, roast duck in four, while roast pork requires for its digestion more than five hours. It must not be supposed, however, that because certain articles of food are slowly digested, that necessarily they will give rise to uneasiness or inconvenience in the stomach, but there are times when the administration of food, with reference to its rapid digestion, becomes of vital importance. Thus, in certain critical periods of disease, when a life hangs upon a thread, when every moment that vitality can be prolonged is invaluable, the judicious administration of food that can be easily and quickly digested and absorbed may be the only means of saving the patient. It must be borne in mind that the natural stimulus of the gastric juice is the presence of food, and that for the time being there is a limit to the amount of this secretion, like all others. Hence, whenever there have been great prostration of strength and loss of tone, the stomach, enfeebled like the rest of the body, can digest but little;

<sup>1</sup> A Treatise on the Structure, Economy, and Diseases of the Liver, p. 201. London, 1803.

<sup>2</sup> Beaumont, op. cit., p. 269.

food, under such circumstances, should be given cautiously, both in quantity and quality.

In concluding the subject of gastric digestion attention should be called to the fact that the coats of the stomach itself are unaffected by the action of the gastric juice during life, but are digested after death. It is said that when one of the old alchemists announced that he possessed a universal solvent, the question was at once asked in what did he keep it. Naturally enough it was asked in the last century of those who held that the gastric juice would dissolve organic substances, why it did not act upon the stomach itself. We have seen, however, that the gastric juice does not digest all kinds of organic food, but that its action is limited rather to particular kinds of it, it having no action upon fat and starch, for example. The answer would then appear to be, that the stomach is lined with some substance that the gastric juice does not act upon at least during life, it being well known that tripe, for example, or the mucous membrane of the calf will be digested when taken as food by another animal.

John Hunter<sup>1</sup> showed, in 1772, and others since, that the stomach, or more particularly the cardiac part of it, in man and animals dying suddenly, was digested by its own gastric juice after death. Hunter's explanation of the phenomena was that during life the vital principle protected the stomach from the dissolving influence of the gastric juice, but that after death, the vital principle being no longer present, the gastric juice produced its characteristic effect. This so-called explanation is equivalent to saying that the stomach is not digested during life and is digested after death, a mere restatement of the fact of which we wish to learn the cause, not an explanation of it.

Pavy<sup>2</sup> argued that the alkalinity of the blood in the stomach during life neutralized the acidity of the gastric juice and hence protected the stomach. This observer endeavored to demonstrate the truth of his explanation by ligating all the gastric vessels in a rabbit and so depriving the stomach of its alkaline blood and then subjecting it to the action of its acid gastric juice. But under such circumstances the stomach is practically dead, and we know that a dead stomach will be digested. Pavy's so-called explanation is only a demonstration then that a dead stomach will be digested, not an explanation of the fact. Further, that this is not the true explanation is shown from the fact that sometimes the alkaline intestinal secretion will act upon the coats of the intestine permeated with alkaline blood in the same manner as the gastric juice acts upon the stomach.

According to Profs. Dalton<sup>3</sup> and Flint,<sup>4</sup> it is impossible for the gastric juice to act upon the stomach so long as the catalytic changes incident to nutrition, etc., are going on, but that after death these catalytic changes having ceased then the gastric juice will act. Apart from it being well known, however, that the so-called catalytic changes incident to nutrition going on in the living frog's legs or in the living rabbit's ear, do not prevent these parts being acted upon when passed into the

<sup>1</sup> Phil. Trans., London, 1772.

<sup>3</sup> Physiology, 2d edit., 1861, p. 132.

<sup>2</sup> Phil. Trans., London, 1863.

<sup>4</sup> Physiology, vol. ii. p. 281.



stomach of a living dog in which a fistulous opening has been made, it appears to us that this explanation differs only from Hunter's in using the word catalysis instead of vital spirit. To offer as an explanation of the immunity enjoyed during life by the coats of the stomach from the effects of the gastric juice, the antagonism of a catalytic action, is, like Hunter's, only a restatement of the fact to be explained.

Bernard<sup>1</sup> taught that the living epithelium of the stomach protected it from the gastric juice, assuming that the epithelium was as constantly renewed as destroyed. According to Pavy,<sup>2</sup> however, the mucous membrane can be removed in a living animal, and the coats of the stomach, though exposed, are yet unaffected by the gastric juice. This experiment, however, does not seem to apply to man, for pathological facts, like the round ulcer of the stomach, would seem to show that in the absence of the epithelium the parts beneath are affected during life by a kind of corrosion due to the gastric juice. A confirmation of the view that the epithelium-lining of the stomach gives it its immunity from digestion during life, is shown by the fact that worms, like the thread-worm, *ascaris*, etc., whose body wall is covered with epithelium are able to live in the stomach, bathed at times in gastric juice. After the death of the worm, from any cause, the mouth or anus being opened, then the gastric juice is able to penetrate within its body and will then act upon the viscera until often nothing will be left of the worm except its outer body wall, which will float about in the stomach, unaffected by the gastric juice. In the same way, if the epithelium of the stomach be loosened from the parts beneath, it will be found undigested in the gastric juice; as a matter of fact, it is not digested whether living or dead any more than the skin of the *ascaris* is digested. There is no reason for assuming, then, that during life it is rapidly regenerated because it is constantly being destroyed. After death the epithelium loosening itself from the coats of the stomach, the latter will no doubt be attacked by the gastric juice as long as the temperature is maintained at 100° F., the epithelium itself remaining unaffected. This explanation has at least one advantage—that it does not call upon vital spirits, catalysis, or similar fetich ideas, to explain a phenomenon of digestion, but depends simply upon the chemico-physical fact as to whether or no epithelium is digested in gastric juice.

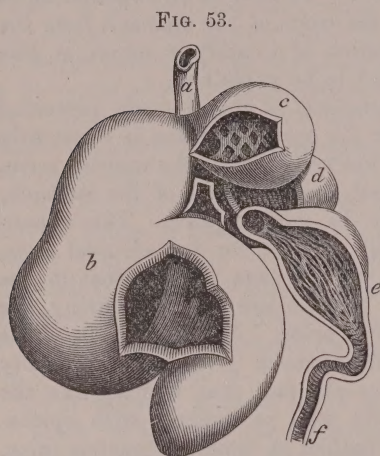
In concluding the subject of gastric digestion it may not be superfluous to notice that the alimentary canal of man, as a whole, is intermediate in character between that of the carnivora and herbivora, furnishing another proof in addition to those already given, that the natural diet of man is a mixed one. The food of an herbivorous animal or vegetable feeder consisting of grass, leaves, roots, etc., contains comparatively little nutriment, and, therefore, a great quantity of it must be eaten. This necessarily entails a long and capacious alimentary canal with special modifications in different parts of it, the effect of which is that the maximum amount of nutriment is obtained from the food. Thus when the stomach of a ruminating animal, like the llama (Fig. 49), or giraffe (Fig. 82), is compared with that of man, it will be observed that

<sup>1</sup> *Physiologie Experimentale*, tome ii. p. 404. Paris, 1856.

<sup>2</sup> *Op. cit.*, p. 163.

the stomach of the ruminant is subdivided into four compartments (Fig. 53, *b, c, d, e*), the last of which, the abomasum, communicating with the

small intestine, corresponds with that of man, and secretes the gastric juice. Of the other three stomachs, the rumen (*b*) is the largest, and together with the reticulum (*c*) or honeycombed stomach (not seen in Fig. 49) receives the food after it has been chewed and insalivated. After a few moments, however, a bolus of food will be regurgitated into the mouth and there thoroughly masticated and insalivated. The second time, however, that it is swallowed the food passes directly into the third stomach, the psalterium (*d*) or monyplies. This is effected by means of a musculo-valvular arrangement at the mouth of the



Compound stomach of an ox. *a.* Oesophagus. *b.* Rumen, or first stomach. *c.* Reticulum, or second. *d.* Omasus, or third. *e.* Abomasus, or fourth. *f.* Duodenum. (From RYMER JONES.)

bolus of food directly from the oesophagus into the psalterium, whence it passes into the abomasum (*e*) or fourth stomach and thence into the intestine. By this arrangement of the rumen, etc., the thorough mastication and insalivation of the food are insured, while the psalterium or third stomach acts as a filter or strainer, its mucous membrane being raised up into folds, like the leaves of a book, permitting only finely divided or semi-liquid matter to pass into the abomasum. Were not the food thus thoroughly digested much of its nutritive value would be lost.

The stomach of a meat eater, on the other hand, is as simple as that of man, while its intestines are not as long, its food being so much more nutritious as compared with that of the vegetable feeder.

We have seen why a strictly meat diet should be avoided in man as well as a vegetable one, hence his alimentary canal will not be as simple as that of the one nor as complicated as that of the other, but intermediate in character between the two.

The further illustration of this subject brings us, however, to a consideration of the intestines, to which let us now turn.



## CHAPTER X.

### INTESTINAL DIGESTION. INTESTINAL JUICE. PANCREATIC JUICE. LIVER. GLYCOGEN. BILE. FECES. DEFECATION.

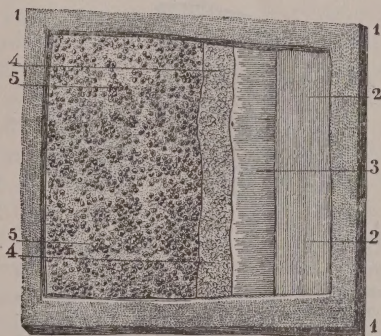
WE have seen that shortly after food is taken into the stomach it passes in small quantities through the pyloric orifice into the small intestine, or the part of the alimentary canal intervening between the stomach and the ilio-cæcal valve. The small intestine is a cylindrical tube and in situ measures on an average from fifteen to eighteen feet, but when separated from the mesentery or the peritoneum, which holds it in position in the abdominal cavity, it will be found to be a little longer—about twenty feet. It has a diameter of about one and a quarter inches.

The small intestine is composed, in addition to its external or peritoneal coat, of two others: of a mucous membrane, including an epithelial and submucous or fibrous coat (Fig. 54, 4, 5), and of a muscular coat lying exteriorly between the peritoneum and the mucous membrane. The muscular coat consists of unstripped muscular fibre, arranged in two layers, longitudinally or parallel with the long axis of the intestine, and circularly or at right angles with the axis (Fig. 54, 2, 3); the circular fibres being better developed than the longitudinal ones.

It is through the slow and gradual contraction and relaxation of these muscular fibres, the so-called peristaltic or vermicular movement, that the food is propelled along the intestine, the contraction of the circular muscular fibre at the pyloric orifice preventing regurgitation into the stomach.

Like the movements of the stomach, the natural stimulus to the vermicular motion of the intestine is the presence of food, during the intervals of digestion the intestine being at rest. The peristaltic or vermicular motion of the intestine can be well seen by opening an animal in full digestion. What is positively known, however, of the intestinal movements in man is derived from pathological cases where the abdominal walls were so thin that the motion could, to a certain extent, be seen and felt, or from cases of

FIG. 54.



Portion of the duodenum, viewed from without, natural size. 1. Thickness of the duodenum. 2, 3. Longitudinal and transverse layers of fibres of the muscular coat. 4. Fibrous coat. 5. Exterior of the mucous membrane, with the duodenal glands imbedded. (LEIDY.)

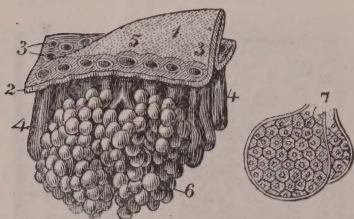
intestinal fistula like that under the care of Busch, which will be referred to again shortly. The gradual passage of the food through the alimentary canal is no doubt, as suggested by Longet,<sup>1</sup> facilitated by the gases, nitrogen, oxygen, carburetted hydrogen, which are constantly found there, the canal being kept distended and its walls supported in this way.

As the food passes into the small intestine it becomes incorporated with the bile, the pancreatic and intestinal juices, the first two secretions pass into the duodenum from the liver and the pancreas respectively; the last, however, is secreted by glands found all through the intestinal tract. While the further changes that the food undergoes in the small intestine are due to the simultaneous effects of the bile, pancreatic and intestinal secretion, it is better, however, to study the effects of each of these secretions separately whenever possible in order to ascertain their relative importance in digestion? We will begin, then, with the intestinal juice.

### INTESTINAL JUICE.

The succus entericus, as it is also called, is secreted by two kinds of glands, the glands of Brunner or Brunn and the follicles of Lieberkühn. The former are confined to the duodenum; the latter, however, are found not only in the small intestine but in the large intestine also.

FIG. 55.



A vertical section of the duodenum highly magnified. 1. A fold-like villus. 2. Epithelium of the mucous membrane. 3. Orifices of the tubular glands, 4. 5. Orifice of a duodenal racemose gland, 6. 7. Two vesicles of the latter, more highly magnified, exhibiting the epithelial cells lining their internal surface. (LEIDY.)

The duodenal glands of Brunner (Fig. 55) are of the racemose type of gland; they average about the  $\frac{1}{10}$ th of an inch in diameter and to the naked eye appear like little round bodies in the submucous tissue. The excretory duct, which transmits the secretion from the grape-like masses of which the gland consists, pierces the mucous membrane and opens into the cavity of the intestinal canal.

According to Hirst and Heidenhain,<sup>2</sup> the cells of Brunner's glands exhibit essentially the same changes during periods of rest and activity as those of the pyloric tubules of the stomach, being large and clear during the period intervening between meals and small and cloudy during digestion, the secretion being elaborated during the former period and poured out during the latter.

The reaction of the secretion is alkaline. According to Grutzner,<sup>3</sup> it will digest fibrin in an acid solution, and Budge<sup>4</sup> and Krolow state that a watery extract will convert starch into sugar. Beyond these facts nothing is known positively of the properties of the secretion of Brunner's glands.

<sup>1</sup> Physiologie, 1873, tome I, p. 166.

<sup>3</sup> Pfüger's Archiv, Band xii, S. 288.

<sup>2</sup> Hermann: Physiologie, Funfter Band, S. 163.

<sup>4</sup> Hoppe-Seyler: Phys. Chemie, S. 270.



By far, however, the greatest quantity of the intestinal juice is secreted by the follicles of Lieberkühn, otherwise known as the simple tubular glands of the intestine. These glands resemble somewhat the pyloric tubules of the stomach, consisting of a basement membrane lined with a single layer of columnar cells. The tubules having a diameter of about  $\frac{1}{360}$ th of an inch, extend through the mucous membrane, which is about  $\frac{1}{75}$ th of an inch thick, their fluid ends look toward the muscular coat, their mouths opening into the cavity of the intestine. The secretion of these tubules will therefore pass into the interior of the intestine. The tubules are as closely packed together as possible and are only absent in that part of the duodenum where the glands of Brunner are found, and in the remaining part of the small intestine, the so-called jejunum and ileum<sup>1</sup> in the position of the Peyer's patches and solitary glands, and even here they are not entirely absent.

From the immense number of these tubules one would infer that a very considerable quantity of intestinal juice is secreted. The exact amount daily poured into the intestine has never been accurately determined; it does not appear to be, however, as much as we would have anticipated.

The reaction of the intestinal juice is alkaline, but as it is very doubtful whether normal intestinal juice has ever been collected in any animal or man it is not worth while to consider in detail its composition. Probably it is composed of water, salts, and some albuminous principles. It is true that numerous experiments have been made upon animals with the object of obtaining the intestinal juice, of determining the quantity secreted, its composition, and effects upon food, etc. These experiments unfortunately, however, were not made under physiological conditions, hence the results obtained are of little value as illustrating digestion in the animal experimented upon and practically useless in their application to man. Frerichs,<sup>2</sup> for example, experimented in this way. A loop of the small intestine of a living cat or dog was withdrawn from the abdomen during the interval of digestion. The loop was four to eight inches in length, was isolated from the rest of the intestine by a ligature. It was opened and washed and then replaced in the abdomen. Some hours afterward the animal was killed and the contents of this isolated portion of the intestine examined. It was found to contain a fluid which was assumed to be intestinal juice. It is probable, however, that during the intervals of digestion no intestinal juice is secreted, the natural stimulus to the secretion being the presence of food, as is the case in the secretion of the gastric and pancreatic secretions and the bile. Further, the method of experimenting made use of by Frerichs involves, necessarily, the ligating and division of the vaso-motor nerves of the intestine with the consequent changes in the circulation and nutrition of the parts. The fluid obtained being, therefore, abnormal, it is not necessary to describe its properties.

<sup>1</sup> The distinction between jejunum and ileum is entirely an artificial one, there being no difference structurally between the two. The small intestine naturally divides itself into duodenum and ileum, distinguished by the former containing the glands of Brunner, the latter the patches of Peyer. More than three hundred years ago Vesalius observed (*De corporis humani fabrica Libri septem*, p. 609. Basil, 1543) "Qua propter quis jejunum habendus sit finis, aut quod ilei principium, non statuo." The name jejunum being therefore a meaningless one, ought long since to have fallen into disuse.

<sup>2</sup> Wagner: *Physiologie*, 1846, Band iii. S. 581.

Bidder and Schmidt<sup>1</sup> adopted a different plan from that of Frerichs. These investigators cut off the bile and the pancreatic juice from the intestine by ligating the bile and pancreatic ducts and then introduced food with the object of studying the effects of the intestinal juice upon it. It is questionable, however, after such an operation, whether digestion is normal, and even if it were, the results of feeding cats and dogs operated upon in this way upon vegetable articles of food, like starch, etc., could hardly be expected to throw much light upon intestinal digestion as it takes place in man.

Colin's<sup>2</sup> experiments not differing essentially in principle from that of Frerichs's, it would be superfluous to describe in detail his results, or those obtained by the method of Thiry.<sup>3</sup> The latter consisted in cutting a piece out of the intestine, and after joining the lower end of the upper part of the intestine to the upper end of the lower, of attaching the isolated cut out portion, its nerves and vessels being undisturbed, by its open end, to the fistulous opening in the abdominal walls, the other end being closed.

Were our knowledge of the properties of the intestinal juice in man dependent upon the experiments that have been made upon animals, we would know positively next to nothing about it. Fortunately, however, for physiology, there occurred some years ago a case of intestinal fistula in a woman which proved to be for intestinal digestion, what St. Martin's case was for gastric digestion. It is true that the observations of Busch, who had charge of the case, are not by any means as extended or complete as those of Beaumont; nevertheless, they are invaluable to us, as what is known of the action of the intestinal juice during digestion in man is almost entirely based upon them.

Busch<sup>4</sup> tells us that a woman, thirty-one years of age, in the sixth month of her fourth pregnancy, being tossed by a bull, was wounded in the abdomen. The wound was situated between the umbilicus and pubes, and consisted of two contiguous openings communicating with the intestinal canal. It is probable that these two openings were in the upper third of the small intestine.

Notwithstanding her ravenous appetite the patient became very much emaciated in consequence of her food passing out of the upper of the two openings just referred to. It occurred to Busch, however, that the life of the woman might be saved by introducing cooked food into the lower opening, or that communicating with the lower portion of the intestine. This plan of treatment proved successful. The nutrition of the patient rapidly improved. The opening, however, not uniting, the woman was made the subject of the observations contained in the paper just referred to.

It will be observed that from the peculiar conditions of the case, food introduced by the mouth, unless absorbed by the stomach, would pass on into the upper portion of the intestine, and so out of the body by the upper of the two openings, having been modified in its course by the saliva, gastric, intestinal, and pancreatic juices and the bile; whereas,

<sup>1</sup> Die Verdauungssäfte, 1852, S. 271.

<sup>3</sup> Wiener Sitzberichte, 1864, p. 77.

<sup>2</sup> Physiologie Comparée, 1854, p. 648.

<sup>4</sup> Virchow's Archiv, 1858, Band xiv. S. 140.



food introduced into the lower of the two openings would be modified by the intestinal juice only, as it passed along the small intestine, and if not digested or absorbed would pass out by the anus unchanged. The conditions of the experiment were, therefore, perfectly physiological.

The intestinal juice was secreted in response to the natural stimulus of the food, while its effect upon the different kinds of food could be studied, either mixed or unmixed with the gastric, pancreatic juices, etc. Necessarily the quantity of intestinal juice obtained at any one time, by the introduction of sponges, etc., was not sufficient to admit of detailed analysis; the reaction was determined, however, to be alkaline. The general results of Busch's<sup>1</sup> observations and experiments upon the intestinal juice may be summed up as follows:

Starch, both raw and hydrated, was invariably converted by it into glucose; cane sugar, however, was not changed into glucose, appearing in the feces as cane sugar. The intestinal juice digested more or less cooked meat and coagulated albumen, but had little or no effect upon fat; the latter when introduced into the lower opening of the intestine is always found in the feces as fat unchanged.

In the case of intestinal fistula lately observed by Demant,<sup>2</sup> starch was converted into glucose, but albuminous substances did not appear to be transformed into albuminose. No effect was observed upon neutral fats, though oily matters containing free acid were emulsified. The results of the observations of Demant confirm in the main those of Busch. It must be remembered, however, that the fistula in the former case was situated much lower than in the latter, and that the experiments upon the different kinds of foods were performed outside of the body after the intestinal juice had been drawn from the fistula. The observations of Busch were, therefore, made under more strictly physiological conditions than those of Demant, and deserve greater confidence.

It will be seen, therefore, that the action of the intestinal juice in digestion is of a supplementary character, reinforcing the effects of the saliva upon starch, and of the gastric juice upon the albuminoids, it having no effect, however, upon cane sugar or fat.

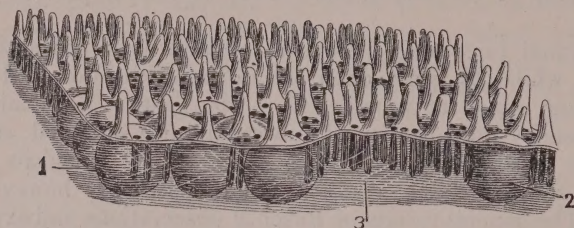
Before turning to the consideration of the remaining digestive secretions, attention should be called to a peculiar disposition of the mucous membrane of the intestine, which, to a certain extent, retards the passage of the food and exposes it longer to the digestive fluids and to a greater absorbing surface. I refer to the villi and the valvulæ conniventes. On opening the small intestine and gently washing it, one will observe that instead of it being smooth, it presents a velvety appearance. This is due to the mucous membrane (Fig. 56) being raised up into millions of little cones or cylinders, the villi, which project inwardly into the cavity of the intestine. As these little structures are intimately connected with the subject of absorption, our account of their anatomy will be deferred until the next chapter, merely mentioning them here as offering a certain amount of resistance to the passage of

<sup>1</sup> Op. cit., S. 186.

<sup>2</sup> Virchow's Archiv, 1879, Band lxxv S. 419.

food, just as any roughened surface offers resistance as compared with a smooth one to a substance passing over it.

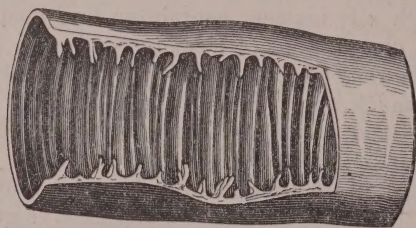
FIG. 56.



Portions of the mucous membrane from the ileum, moderately magnified, exhibiting the villi on its free surface, and between them the orifices of the tubular glands. 1. Portion of an agminated gland. 2. A solitary gland. 3. Fibrous tissue. (LEIDY.)

While the villi are found all through the small intestine, the *valvulæ conniventes*, which have the same function in this respect, are restricted to a certain portion of it, being absent in the upper half of the duodenum and in the lower third of the ileum. The *valvulæ conniventes* (Fig. 57) are duplicatures of the mucous membrane extending trans-

FIG. 57.



Portion of small intestine laid open to show *valvulæ conniventes*. (BRINTON.)

versely across the intestine at right angles to its long axis, and occupying usually one-third or a half of the circumference, and sometimes extending all around the tube. The folds are widest in the middle, measuring often from one-quarter to one-half of an inch. On either side of the middle line they thin away until they are lost in that part of the mucous membrane attached to the muscular coat. Inasmuch as there can be counted usually over 800 of these folds, it can be readily understood how the extent of the mucous membrane is increased by them. Naturally the food will take a longer time to pass over and between these barriers, so to speak, than over a plane surface, and this is of advantage in digestion and absorption, as the food will be more thoroughly incorporated with the secretions and have a better chance of being absorbed.

It is often stated that the *valvulæ conniventes* are only found in the intestine of man, this is erroneous; they are present, as Bischoff has shown, in the gorilla, and the author in the chimpanzee;<sup>1</sup> they are

<sup>1</sup> Proceedings Acad. Nat. Sciences, Philadelphia, 1880, p. 166.



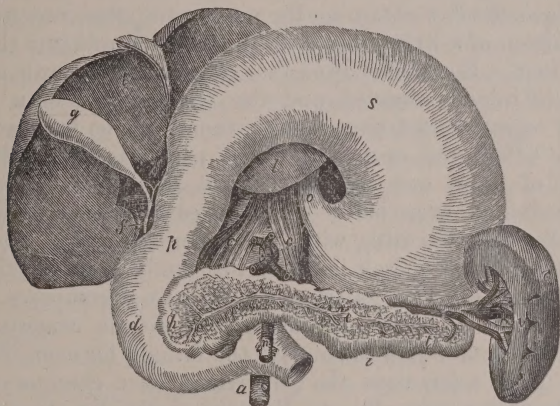
also found in the ox, llama, camel, elephant, in the ornithorhynchus, and are well developed in the shark, giving rise in the latter animal to the so-called spiral valve.

Merely mentioning that the solitary glands and patches of Peyer will be described when the subject of the blood is considered, let us pass on now to the consideration of the pancreatic juice and the bile, and of the rôle that these secretions play in digestion.

### PANCREATIC JUICE.

The pancreas, in its general structure, resembles so closely the parotid and submaxillary glands, that it was known to the older anatomists as the abdominal salivary gland (Fig. 58). It is situated in the upper and

FIG. 58.



View of the pancreas and surrounding organs. 1-5th. *l.* The under surface of the liver. *g.* Gall-bladder. *f.* The common bile-duct. *s.* The stomach. *d.* Duodenum. *h.* Head of the pancreas. *t.* Tail, and *i.* body of that gland. Pancreatic duct (*e*) and its branches. *r.* The spleen. *v.* The hilus. *c, c.* The crura of the diaphragm. (QUAIN.)

posterior part of the abdominal cavity, behind the stomach and between the duodenum and the spleen. It is about seven inches long, and an inch and a half broad, and from half an inch to an inch thick. It usually weighs about three to four ounces, and in its minute structure is of the racemose type. Its duct in man passes into the duodenum by a common orifice with the ductus choledochus, three or four inches below the pylorus. Not unfrequently there is also a supplementary pancreatic duct opening into the duodenum a little above the main duct.

The secretion of the pancreas, or the pancreatic juice, has never been obtained from man. Probably it is very much like that of the pancreatic gland of the dog, which, according to Bernard,<sup>1</sup> consists of water, an organic substance (pancreatin), and salts. With the exception of what has been learned from pathological observations, nothing is known of the effect of the pancreatic juice upon food during digestion in man,

<sup>1</sup> Physiologie Experimentale, tome ii. p. 237. Paris, 1856.

and such observations would be inconclusive unless viewed by the light of experiments upon animals and comparative anatomy.

The first physiologist, so far as known to the author, who attempted to obtain the natural pancreatic juice from a living animal, was Regnerus de Graaf,<sup>1</sup> who, in 1662, opened the intestine of a dog and introduced a duck's quill into the orifice of the pancreatic duct. According to Bernard,<sup>2</sup> however, the fluid obtained by de Graaf was not pancreatic juice, being acid in reaction, whereas the normal pancreatic juice, according to Bernard, is alkaline. Majendie<sup>3</sup> repeated de Graaf's experiment, but with not much success. Leuret<sup>4</sup> and Lassaigue, in 1824, and Tiedemann and Gmelin,<sup>5</sup> in 1827, obtained what they supposed to be the natural pancreatic juice from the horse and dog, but nothing was learned of its physiological properties from their experiments. Little or nothing was known of the natural pancreatic juice up to the year 1846, when Bernard obtained the pancreatic juice of the dog, and investigated its properties.

Bernard's method<sup>6</sup> of obtaining the pancreatic juice consisted in opening the abdomen of a living dog and inserting a canula into the principal pancreatic duct. Bernard showed that during the intervals of digestion no pancreatic juice is secreted, and that the organ is of a pale color. The animal experimented upon should, therefore, be fed moderately an hour or so before the operation. The pancreas then becomes rose colored, full of blood, and secretes a viscid alkaline juice, which flows into the duodenum, even before the digested food gets there from the stomach. In experimenting with the pancreatic juice thus obtained, Bernard showed that it was important to study its properties as soon as possible, for, unlike the gastric juice, it soon decomposes. Another difference between a pancreatic and gastric fistula consists in the impossibility of maintaining permanently the former, for even if the canula remains in place a few days the pancreatic juice changes entirely its character, becoming, according to Bernard, decidedly abnormal. This change takes place usually in a few hours, and so sensitive is the pancreas, that sometimes the secretion is abnormal, even when first drawn.<sup>7</sup>

Apart from the impropriety of assuming that the pancreatic juice of man and the dog are necessarily identical, one might reasonably doubt even whether the secretion obtained by Bernard's method always really represents the normal pancreatic juice in the dog, the pancreas being so readily inflamed and irritated by the operation. It is probable, however, that the secretion obtained by Bernard was normal, and that his conclusions in reference to the properties of the secretion and functions of the pancreas generally are in the main correct, as they accord pretty well with what the facts of comparative anatomy and pathology, and the results of experiments with artificial pancreatic juice teach us of the functions of the gland.

It is well known that in the rabbit the pancreatic duct opens separately into the intestine twelve inches below the bile-duct, instead of by

<sup>1</sup> Opera Omnia, 1678, p. 292.

<sup>3</sup> Physiologie, p. 367. Paris, 1816.

<sup>5</sup> Op. cit., p. 27.

<sup>7</sup> According to the later observations of Berstein, it appears, however, that a permanent pancreatic fistula can be maintained. Ludwig's Arbeiten, 1869.

<sup>2</sup> Op. cit., p. 176.

<sup>4</sup> Op. cit., p. 102.

<sup>6</sup> Op. cit., p. 190.



an opening common to it and the bile-duct, as is the case in man or the dog; Bernard<sup>1</sup> tells us that after feeding a rabbit with fat he noticed that it was only below the entrance of the pancreatic duct into the intestine that the lymphatics of the small intestine or lacteals contained any fat. This observation not only suggested to Bernard the idea that the pancreatic juice emulsified the fat—that is, reduced it to a fine state of subdivision, and so rendered it absorbable—but was also the starting-point of his researches upon the functions of the pancreas generally.

While it is true that in the rabbit, as a general rule, emulsified fat is only found in the lymphatics below the entrance of the pancreatic duct, this is not invariably so, as according to Bidder and Schmidt,<sup>2</sup> and our own observations, emulsified fat is at times found in the lymphatics above this point. While the rabbit is a convenient animal for making Bernard's experiment, it may be mentioned in this connection that the beaver, though a rarer animal, presents even a more favorable disposition for making the observation than the rabbit, the pancreatic duct in this rodent opening eighteen inches below the bile-duct. Having examined several beavers in full digestion, the author noticed also that in some cases, as in the rabbit, the lymphatics contained chyle, both above and below the entrance to the pancreatic duct. Even if it were true that fat never is emulsified in the rabbit, except by the pancreatic juice, it would not prove that the pancreas is indispensable in the digestion of fat either in man or animal. Fat, as such, not being the natural food of the rabbit, there is no necessary connection between it and its pancreatic juice; while in many fish, whose food contains fat, the pancreas is absent. In birds, also, the fat is usually absorbed by the mesenteric bloodvessels in general, and not by the lymphatics of the small intestine.

Eberle,<sup>3</sup> however, showed, in 1834, that an artificial pancreatic juice, prepared by making an infusion of the pancreas, would emulsify oil when mixed and agitated with it, and Bernard,<sup>4</sup> apparently without knowing of Eberle's views, proved that the pancreatic juice of the dog, obtained by a fistula, would do the same, about two parts of the pancreatic juice of the dog, by weight, emulsifying one part of oleaginous matter.

These experiments with the artificial and natural pancreatic juice and the facts of comparative anatomy just referred to, show conclusively that while the pancreatic juice emulsifies fats and so promotes their absorption, the pancreatic secretion is not indispensable, fat being digested and absorbed even in the absence of the pancreas. The digestion and absorption of fat must, therefore, be affected by other secretions as well as by the pancreatic juice. Let us see whether pathology throws any light upon this question.

In a number of cases reported by pathologists in which there was disease of the pancreas in human beings, it was observed that a fatty diarrhoea was present during life, and such is the case also to a certain

<sup>1</sup> *Op. cit.*, p. 179.

<sup>3</sup> *Die Verdauung*, S. 251. Würzburg, 1834

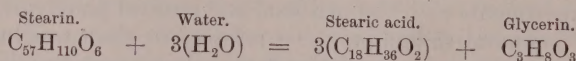
<sup>2</sup> *Die Verdauungssäfte*, S. 55. Leipzig, 1852.

<sup>4</sup> *Op. cit.* p. 257.

extent in animals in which the pancreas has been destroyed, as shown by Bernard<sup>1</sup> and others.

Such cases and experiments are often offered as proofs of the influence exerted by the pancreas in promoting the digestion and absorption of fats. It is interesting in this connection, however, that Brunner,<sup>2</sup> who was the first, so far as the author is aware, to destroy the gland in a living animal, states in his work on the pancreas that he succeeded in keeping a dog alive three months after the pancreas had been extirpated, and that yet he found the feces normal. Further, it is well known also that often in cases of fatty diarrhœa the pancreas has been found after death healthy, the liver being the diseased organ, and that occasionally both pancreas and liver are affected at the same time.<sup>3</sup> Indeed, so often is the liver affected in such cases that fatty diarrhœa is regarded as much a symptom of hepatic as of pancreatic disease. The conclusion from such cases would seem to be that the bile emulsifies the fats to some extent at least as well as the pancreatic juice. And this is in accordance with the fact already mentioned, of finding emulsified fat occasionally in the lymphatics of the rabbit above the entrance of the pancreatic duct. In the case of the intestinal fistula observed by Busch, it will be remembered that the food that was taken in the mouth passed out of the upper of the two openings of which the wound consisted. According to Busch,<sup>4</sup> when fat was taken in by the mouth it passed out of the upper opening in the state of a fine emulsion. This change in the fat must then be due in man to either the pancreatic juice, bile, or the intestinal juice. But we have seen, according to Busch, that fat introduced into the intestine through the lower opening of the wound appeared in the feces unchanged. The intestinal juice, or at least that part of it secreted by the follicles of Lieberkühn, cannot be supposed to emulsify the fat. This function, then, must be performed by either the pancreatic juice or the bile, or both, unless the secretion of Brunner's glands is hereafter shown to exert such an influence.

An important observation made by Bernard<sup>5</sup> was that the alkaline pancreatic juice out of the body, when mixed with a neutral fat, decomposed the latter into glycerin and a fatty acid, the phenomenon being evidently one of hydration in presence of a ferment as follows:



If this change takes place in the human intestine, which is very probable, it will account for the presence of the palmitates and oleates found in the blood and feces, as soap—that is, a fatty acid combined with alkali.

It is admitted by all physiologists that the pancreatic juice transforms starch instantaneously into glucose, one part of pancreatic juice by weight being required for the conversion of 4.5 parts of starch. This function of the pancreatic juice was first demonstrated in 1844 by Valentin,<sup>6</sup> who experimented with an artificial pancreatic juice prepared by making a watery infusion of the gland. Bernard<sup>7</sup> showed that the

<sup>1</sup> Op. cit., p. 276.

<sup>2</sup> Experimenta nova circa Pancreas, p. 12. Amst., 1673.

<sup>3</sup> Milne Edwards: Physiologie, tome vii. p. 76. Longet: Physiologie, tome i. p. 291.

<sup>4</sup> Op. cit., S. 175.

<sup>6</sup> Lehrbuch der Physiologie, S. 356. Braunschweig, 1847.

<sup>5</sup> Op. cit., p. 257.

<sup>7</sup> Op. cit., S. 329.



natural pancreatic juice had the same effect in a very marked degree. Since at least nearly one-half of the food of man consists of starch, this function of the pancreatic juice is a most important one.

We have seen that cane sugar is very slowly converted into glucose in the stomach, but in such small quantities that we must look for its further digestion in the small intestine. The case reported by Busch<sup>1</sup> shows that the transformation of cane sugar into glucose in the intestine is due to the pancreatic juice, for the bile has no such effect, nor the intestinal juice, while when cane sugar was introduced into the mouth glucose appeared at the upper opening of the wound; when cane sugar was introduced into the intestine by the lower opening of the wound it appeared unchanged in the feces. Cane sugar is, however, converted into glucose by artificial intestinal juice. In addition to the effects of the pancreatic juice upon the kinds of food already referred to, it has also the property of assisting the digestion of albuminous substances, about one part by weight of pancreatic juice digesting eight of albuminous substances. This effect of the pancreatic juice was first demonstrated by Eberle<sup>2</sup> in 1834, with an acidulated infusion of the tissue of the pancreas. Afterward Bernard,<sup>3</sup> in his investigations of the pancreas, called attention again particularly to this fact.

While the albuminous substances are converted into peptones by the pancreatic juice it appears that no intermediate stage like sytonin is formed, as we saw was the case in the digestion of albumen by gastric juice, and, further, that this action of the pancreatic juice is rather of a secondary character, as a considerable portion of the albumen is only converted into leucin and tyrosin.

Inasmuch as the pancreatic juice effects important changes in the fats, starches, sugar, and albuminoids, it might be supposed from the fact of the albuminous substances of the pancreatic juice possessing such different properties that it was a compound rather than a simple substance. Chemists have shown pretty conclusively that such is the case, that the organic matter consists of three principles, pancreatin converting starch into glucose, trypsin transforming albumen into albuminose, leucin, tyrosin, etc., and a third substance, as yet unnamed and not as well understood as the other two, decomposing the fats into glycerin and fatty acids.

As regards the formation of leucin and tyrosin by the action of the pancreatic juice, it should be mentioned that a far greater quantity of these substances is formed outside of the body in digestion with pancreatic juice than within it.

It has been learned from the researches of Heidenhain<sup>4</sup> more particularly, that each cell of the pancreas of a dog, for example, after a period of about thirty hours' fasting consists of two zones, an outer zone, which is either homogeneous or delicately striated and readily staining with carmine, and a large inner zone finely granulated and staining with difficulty; the nucleus, situated partly in the outer zone and partly in the inner one, is irregular in form. If the cell be examined, however,

<sup>1</sup> Op. cit., S. 170, 185.

<sup>2</sup> Op. cit., S. 235.

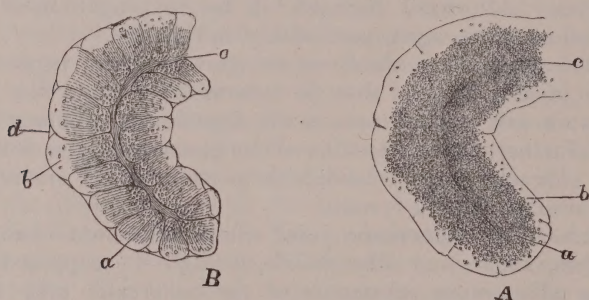
<sup>3</sup> Op. cit., p. 333.

<sup>4</sup> Pflüger's Archiv, 1875, Band x. S. 557. Hermann: Physiologie, Funfter Band, S. 174, 182.

during a period of activity—six hours, for example, after food has been taken—the outer zone of the cell will be found to be the longest, the inner zone in some instances having disappeared altogether, and the whole cell will be seen to have become smaller and staining readily throughout almost its whole extent, through the small size of the inner zone, and the nucleus regular in outline.

The natural inference to be drawn from these observations is, that during secretion the inner zone furnishes either the secretion or the materials of the same, and consequently diminishes in extent in proportion to the activity of the process, while the outer zone enlarges through assimilation of materials brought to the cell by the blood and that the materials of the inner zone are elaborated at the expense of that of the outer one. That such is actually the case appears to have been shown by the observations of Kuhne and Lea,<sup>1</sup> made upon the pancreas of the living rabbit, in which the changes just described were observed as they took place (Fig. 59, A, B).

FIG. 59.



A portion of the pancreas of the rabbit, A at rest, B in a state of activity. *a*. The inner granular zone, which in A is larger, and more closely studded with granules, than in B, in which the granules are fewer and coarser. *b*. The outer transparent zone, small in A, larger in B, and in the latter marked with faint striae. *c* The lumen, very obvious in B, but indistinct in A. *d*. An indentation at the junction of two cells, seen in B, but not occurring in A. (KUHNE and SHERIDAN LEA.)

The fact that a glycerin extract made out of a pancreas taken out of the body while still warm has no digestive effect, whereas the same glycerin extract made out of a pancreas kept for twenty-four hours will digest fibrin, shows that the pancreas contains at the moment that it is taken out of the body but little of its albuminous ferment, but that it does contain a substance readily convertible into such, particularly in the presence of acid, which Heidenhain has called zymogen. If such be the case, it would appear then that the trypsin, the active albuminous ferment of the pancreatic juice, is developed out of the zymogen<sup>2</sup> stored up in the inner zone of the cell, and that the latter is elaborated out of the materials of the outer zone.

As to whether the remaining pancreatic ferments are produced in the same way has not yet been shown. It may be mentioned<sup>3</sup> that the

<sup>1</sup> Verhandl. Nat. Hist. Med. Verien, Band i. Heidelberg, 1877.

<sup>2</sup> Heidenhain : Hermann's Physiologie, Funfter Band, S. 188.

<sup>3</sup> Pfluger's Archiv, Band xiv. S. 465.



pressure under which the pancreatic juice is secreted is about 17 millimetres of mercury.

In concluding our account of the pancreas, its absence in many kinds of fish, in all invertebrates except perhaps the cephalopoda, appears to show that the pancreatic secretion cannot be as indispensable in digestion and absorption as is often supposed.

### THE BILE.

That the bile plays an important part in digestion would be naturally inferred, as suggested by Haller,<sup>1</sup> from the fact that it is poured into the beginning of the intestine; whereas, if it were purely excrementitious in character, it would be eliminated rather at the end of it, in the vicinity of the rectum, for example, or at least separated from the blood without mixing with the food.

It has been shown also by Schwann, Schellbach, Bidder and Schmidt, Arnold, Kuhne, and others,<sup>2</sup> that if the bile is diverted from the alimentary canal by a biliary fistula sooner or later the animal dies. The exceptions to this statement are only apparent, for in those cases where animals have lived for any length of time with a biliary fistula the bile was licked up and swallowed or else double the amount of food was eaten to compensate for the amount of bile lost. Further, it has been well established, by those who have experimentally investigated the subject, that the flow of bile is greatest during digestion. This was shown, for example, by Prof. Flint's observations upon a dog with a biliary fistula.

TABLE XXXVII.<sup>3</sup>—FLOW OF BILE DURING DIGESTION.

| Time.                     | Amount.  | Time.                  | Amount.  |
|---------------------------|----------|------------------------|----------|
| Immediately after feeding | 8.1 grs. | 12 hours after feeding | 5.7 grs. |
| 1 hour after feeding . .  | 20.5 "   | 14 " " "               | 5.0 "    |
| 2 hours " " . .           | 35.7 "   | 16 " " "               | 8.6 "    |
| 4 " " " . .               | 38.9 "   | 18 " " "               | 9.9 "    |
| 6 " " " . .               | 22.2 "   | 20 " " "               | 4.7 "    |
| 8 " " " . .               | 36.5 "   | 22 " " "               | 7.5 "    |
| 10 " " " . .              | 24.4 "   |                        |          |

If the bile were purely excrementitious in character, why should its flow into the intestine be intermittent, or the amount be connected with digestion. A significant fact in reference to the use of the bile in digestion is that in starvation the gall-bladder is usually found distended with bile. If the flow of the bile has no connection with digestion, there would be no reason for this retention. On the other hand, it is well known that if the bile is indefinitely retained, either in animals or man, death takes place; showing that the bile contains some excrementitious material which, under ordinary circumstances, is eliminated from the economy.

That the bile is of use, and yet of no use, is confirmed by the fact already alluded to,<sup>4</sup> that in the doris, one of the mollusca, there are two hepatic ducts, one of which conveys part of the hepatic secretion into the intestine, the other carries the remainder directly out of the body.

<sup>1</sup> *Elementa Physiologiæ*, tomus sextus, p. 615. Lausannæ, 1757.

<sup>2</sup> Funke: *Physiologie*, Erster Band, S. 199. Longet: *Physiology*, tome premier, p. 269.

<sup>3</sup> Flint: *Physiology*, vol. ii. p. 375.

<sup>4</sup> Introduction, p. 37.

Assuming that the bile has some use in digestion, let us see now what is known of its effect upon food.

When bile is mixed with the acid peptones, the result of stomach digestion, a precipitate is formed, but inasmuch as this precipitate is almost instantly redissolved by the alkaline intestinal and pancreatic juice the significance of this fact is not very apparent. Bile has no effect upon cane sugar, while the conversion of starch into sugar by the bile is not constant, being rather due to the mucus that the bile may contain; this effect of the bile is, therefore, insignificant.

There remains only, then, the consideration of the effect of bile upon the fats. For a long time it has been known that bile can be used to take out grease spots in clothing, etc., the bile having the property of dissolving the acid fat. Many physiologists at the present day hold, and with great probability, that the effect of bile upon the fatty articles of food within the intestine is the same as that just mentioned and made use of by scourers and others.

Bile also, to some extent, emulsifies fat, though much less perfectly than the pancreatic juice.

It has been shown by Wistinghausen and Hoffmann<sup>1</sup> that membranes, when moistened with bile, greatly facilitate the passage through them of fat; whereas, when the membranes are moistened with water, the passage of the fat was entirely retarded. We shall see the importance of this observation when we come to study the absorption of fat by the villi.

Admitting that one important use of the bile is the dissolving and emulsifying of fat, and thereby facilitating its absorption, we have an explanation of those cases of fatty diarrhoea observed in men where the liver is diseased, and where the bile is either not secreted or its flow obstructed, and to which we have already called attention in speaking of the function of the pancreas.

The experiments upon animals made by Brodie, Majendie, Mayo, Hawkins, Tiedemann and Gmelin, Leuret and Lassaigne, Bidder and Schmidt, etc., with a view of determining whether the amount of fat absorbed by the lacteals is diminished when the bile is diverted from the intestines, are somewhat discordant.<sup>2</sup> The general conclusion, however, from the observations of these experimenters, seems to be that there is less fat absorbed when the bile is cut off from the intestine, than under the normal conditions. Indeed, according to Leuret and Lassaigne,<sup>3</sup> while a thousand parts of chyle in a healthy dog contain thirty-two parts of fat, there are found only two parts of fat in the chyle of a dog in which the bile has been eliminated by a fistula. Bidder and Schmidt<sup>4</sup> give as the result of their experiments very much the same proportion.

The facts of pathology and experiment then agree in showing that an important function of the bile is to assist the pancreatic juice in preparing the fatty parts of the food for absorption.

It was noticed by Saunders<sup>5</sup> that the bile prevents the putrefaction of the food in the intestine. Since then the majority of experimenters

<sup>1</sup> Milne Edwards: *Physiologie*, tome v. p. 223.

<sup>2</sup> Berard: *Physiologie*, tome ii. p. 364. Longet: *Physiologie*, tome i. p. 274.

<sup>3</sup> *Recherches sur la Digestion*.

<sup>4</sup> *Die Verdauungssäfte*, p. 227.

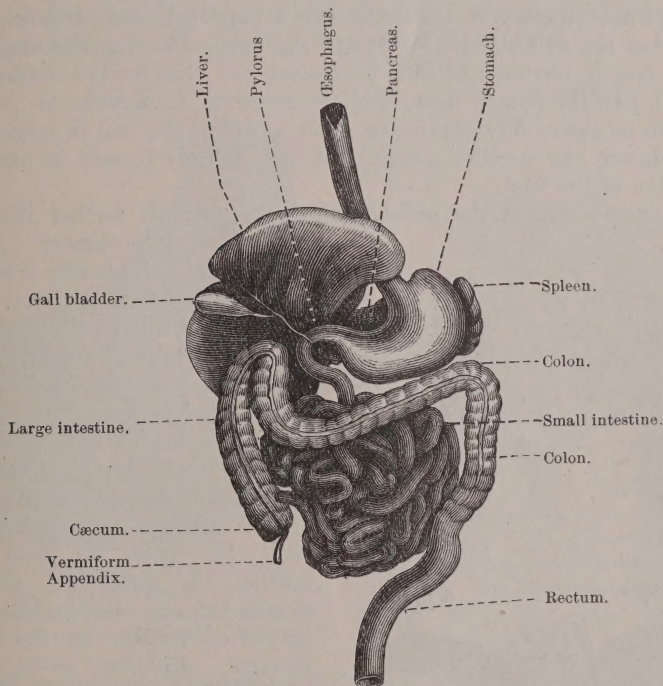
<sup>5</sup> *Diseases of the Liver*, pp. 136, 155, 167, 208. London, 1803.



have noticed that in animals, when the bile is prevented from passing into the intestine, either by ligating the ductus communis or making a biliary fistula, the food becomes putrid, exhaling a very disagreeable and offensive odor, while the gases of the intestine are greatly increased in quantity.

According to Tiedemann and Gmelin, Eberle, Schiff, and other physiologists, the bile exercises a stimulating effect upon the intestine, exciting the peristaltic action and increasing the secretion of the intestinal juices. The want of such stimulus explains, according to those who hold the ancient and plausible view of the bile being a natural purgative, the character of the stools in persons affected with jaundice,

FIG. 60.



Digestive apparatus of man. (MILNE EDWARDS.)

the feces in such cases being passed at long intervals and in a hard condition, through the want of peristaltic action and the softening effect of mixture with the secretions.

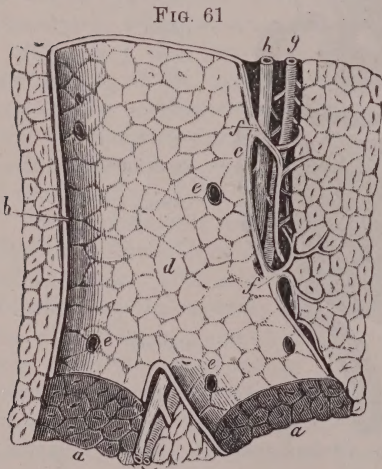
The antiseptic and stimulating action of the bile does not appear to be, however, as indispensable as the changes it produces in the fats.

In connection with the uses of the bile in digestion, a few words about the gall-bladder do not appear superfluous. That the gall-bladder (Fig. 60) is simply a receptacle for the bile seems to be shown from the facts that it is occasionally absent in man without the secretion of bile being suppressed, and that when the cystic duct is either obliterated

or obstructed, no bile is found in the gall-bladder, only mucus then being present. In the intervals of digestion the muscular fibres of the duodenum appear to constrict the orifice of the ductus communis to such an extent as to prevent the flow of the bile into the intestine; the bile then necessarily flows back into the gall-bladder. This can be shown in the cadaver by simply compressing the liver, the effect of which is that the bile flows into the hepatic duct, and thence back to the gall-bladder.

While it cannot be said that there is any invariable rule as regards the presence of or absence of the gall-bladder even in closely allied animals,<sup>1</sup> it being found, for example, in the hog, while absent in the peccary, being present in the antelope though not in the deer, sometimes absent and sometimes present even in the same animal, as in the giraffe; nevertheless, in the carnivora, it may be stated, without exception, that the gall-bladder is always present. The significance of this latter fact is obvious, when it is remembered that while a herbivorous animal, like the cow or deer, eats continuously, a carnivorous one, like the lion or tiger, only obtains its food at intervals, and in large quantities, hence the need of a supply of bile already formed to assist the digestion of the food.<sup>2</sup>

The disposition of the gall-bladder in the python further illustrates its use as a receptacle. In this serpent the gall-bladder is situated some distance from the liver. Were it connected with it, the prey, when introduced into the stomach, would compress the gall-bladder and force the bile into the intestine before the food arrived there, and the effect of the bile upon the food would be lost. The position of the gall-bladder, however, is such that when the food about reaches the duodenum compression is exerted, and the bile passes into the intestine at the proper moment. As Owen<sup>3</sup> well observes, "this fact in comparative anatomy is significant of the share taken by the biliary secretion in the act of chylicification."



Portions of the liver of the hog, exhibiting the lobular structure. The large vessel is a branch of the portal vein, the outlines of the lobules being seen through its transparent wall. The orifices, large and small, seen in the portal vein, are fine branches sent between the lobules. The two vessels lying to the right of the portal vein are branches of the hepatic artery and duct. (LEIDY.)

ing that the amount of bile secreted by the carnivora and man proportionally to the weight to be about the same, there would be from

<sup>1</sup> Milne Edwards: *Physiologie*, tome vi. p. 455.

<sup>2</sup> Cuvier: *Anatomie Comparée*, tome iv. p. 37.

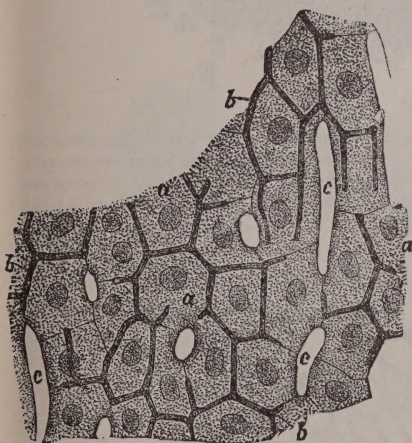
<sup>3</sup> *Comparative Anatomy of Vertebrates*, vol. i. p. 452.



about two and a half to three pounds of bile secreted in twenty-four hours by a man weighing 140 pounds.

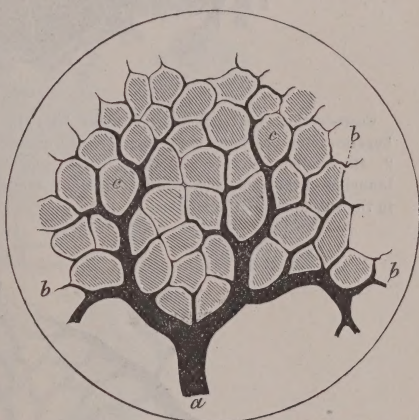
The bile being secreted by the liver, let us now consider the structure of the latter. The liver is the most constantly present gland in the animal kingdom, and is the largest gland in the human body, weighing on an average 3 kil. (50 ozs.). If the surface of the liver be examined, it will be seen to be far from homogeneous, consisting, in fact, of a great number of little masses, the hepatic lobules, varying in diameter from one to two mm. ( $\frac{1}{25}$ th to  $\frac{1}{12}$ th of an inch). The lobules are better seen, however, in the liver of the pig (Fig. 61) than in that of man, and are especially well marked in the liver of the South American capromys. If now one of the hepatic lobules, or acini, be examined microscopically, it in turn will be found to be made up of still smaller nucleated polyhedral masses, the hepatic cells (Fig. 62), varying in diameter from the  $\frac{1}{40}$ th and  $\frac{1}{30}$ th of a mm. ( $\frac{1}{40}$ th to the  $\frac{1}{30}$ th of an inch).

FIG. 62.



Transverse section of part of a lobule from the rabbit's liver. *a, a, a*. Nucleated glandular cells. *b, b, b*. Capillary bile-ducts passing between the adjacent cells. *c, c, c*. Sections of capillary bloodvessels. (GENTH.)

FIG. 63.



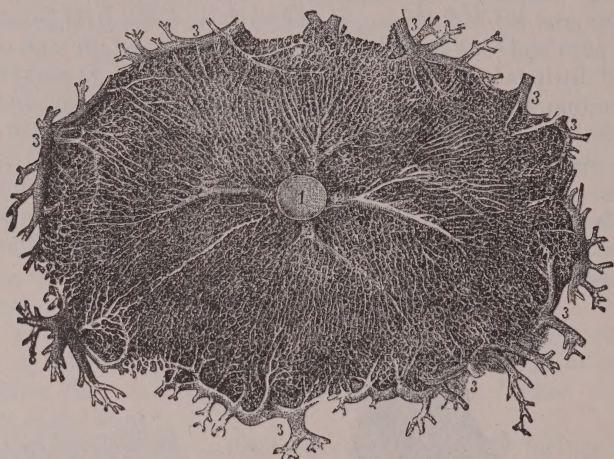
Ramification of portal vein of liver. *a*. Twig of portal vein. *b, b*. Interlobular veins. *c*. Acini. (DALTON.)

Just as the liver is made up of lobules, so each lobule is made up of cells, and as it is through the agency of the cells that the bile is elaborated out of the blood, the manner in which the latter traverses the liver must be next studied.

The liver is supplied with blood by the portal vein and hepatic artery. The portal vein, accompanied by the hepatic artery, entering the liver at the transverse fissure, and dividing and subdividing into numerous branches, ramifies as the interlobular veins (Fig. 63) between the lobules and anastomoses freely around them. From these peripheral interlobular veins arise still smaller ones, the intralobular veins (Figs. 64, 65), which, passing into the lobule from its margin in a radiating manner, unite in the centre as the central vein (Fig. 64). The latter passing directly through the lobule, terminates in the sublobular vein, on which the lobule rests. The various sublobular veins (Fig.

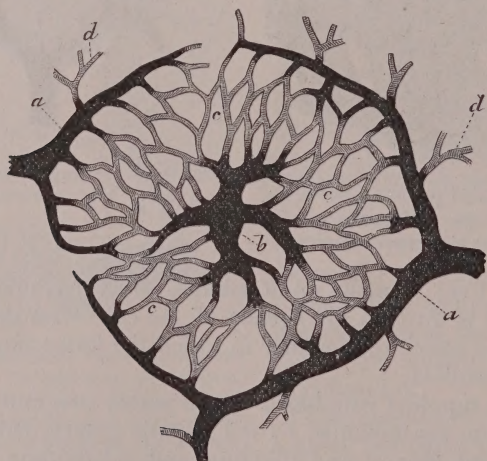
66), in turn uniting together, constitute the hepatic vein. The latter terminates in the ascending vena cava, and leaves the liver at right angles to which the portal vein enters. That the portal and hepatic

FIG. 64.



Cross-section of a lobule of the human liver, in which the capillary network between the portal and hepatic veins has been fully injected. 60 diameters. 1. Section of the intralobular or central vein. 2. Its smaller branches collecting blood from the capillary network. 3. Interlobular or peripheric branches of the vena portæ with their small ramifications passing inward toward the capillary network in the substance of the lobule. (SAPPEY.)

FIG. 65.



Lobule of liver, showing distribution of bloodvessels; magnified 22 diameters. *a, a*. Interlobular veins. *b*. Intralobular vein. *c, c, c*. Lobular capillary plexus. *d, d*. Twigs of interlobular vein passing to adjacent lobules. (DALTON.)

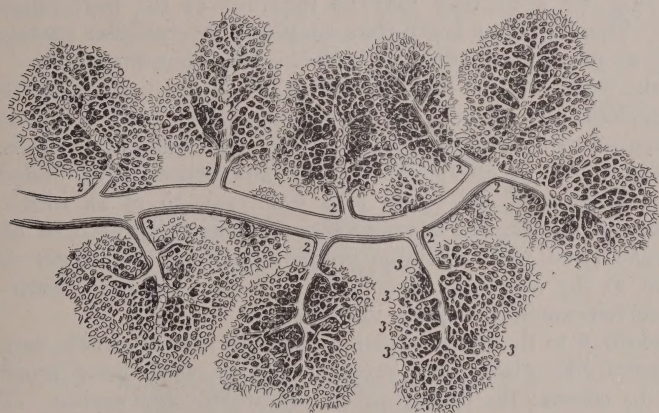
veins are essentially the proximal and distal parts of one and the same vein, is shown not only in the injection of either of them equally well through the other, but also in the manner in which the vascular system



and the liver develop. In the embryo, as we shall see hereafter, at an early period the continuity of the portal and the hepatic veins is quite evident, it not being until later that the connection between the two is obscured by the liver, which grows parasitic-like around the vessels which later supply it with blood. The latter, capillary vessels, constitute then what we have just described in the adult as the interlobular, intralobular (central) and sublobular veins, while that part of the vein which enters the liver is known as the portal vein, that part leaving it the hepatic.

The hepatic artery, after entering the liver, like the portal vein, ramifies between and within the lobules, but unlike the portal vein does not pass through the lobules, but terminates within them in the intra-lobular capillaries. That such is the case, is shown by the injection of the hepatic vein through the hepatic artery. Further, that the liver cells elaborate bile both out of the blood brought to them by the hepatic

FIG. 66.



Injected twig of a sublobular vein passing into the hepatic lobules. About 30 diameters. 1. Small sublobular vein. 2. Central veins passing into the base of the lobules. 3. Their smaller subdivisions. 4. Capillary network of communication with the extreme ramifications of the vena portæ. (SAPPEY.)

artery, as well as by the portal vein, is shown by the fact that the bile is still secreted, even if diminished, if the latter be ligated,<sup>1</sup> and that the bile is secreted even in cases where the portal vein has been found obliterated after death,<sup>2</sup> or passing into the vena cava.<sup>3</sup>

Pathological as well as experimental considerations show that the liver cells are the active agents in the elaboration of the bile. Thus in certain diseased conditions of the liver, noticeable more particularly in the liver of animals, the cells, or the interspaces between them, are found filled with bile,<sup>4</sup> while if a substance like that of sulpho-indigotate of sodium, indigo carmine of the arts, be injected into the circulation of a

<sup>1</sup> Oré Comptes Rendus, tome xliii. p. 463. Paris, 1856.

<sup>2</sup> Andral: Ibid., p. 467.

<sup>3</sup> Abernethy: Phil. Trans., p. 59. London, 1793. Lawrence: Med. Chir. Trans., vol. v. p. 174. London, 1814.

<sup>4</sup> Stiles: Bulletin of the New York Academy of Medicine, 1868, vol. iii. p. 350.

very young mammal, a sucking pig, for example,<sup>1</sup> the liver cells, or the interspaces between them, according to the length of time elapsing between the performing of the experiment and the killing of the animal, will be seen to contain the salt of sodium injected. Since the bile does not exist as such in the blood, it follows that the liver cells not

FIG. 67.

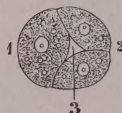


Diagram showing how a few hepatic cells may form a hollow tube. 1. Large cell; viewed from this side the tubes would appear to be the breadth of a single cell. 2. Two cells the diameter of the tube. 3. Passage-way for the bile. (LEIDY.)

only eliminate from the blood the principles of which the bile consists, but also elaborate the same into bile.

The bile having been elaborated by the liver cells out of the blood flowing within the vessels situated at the angles formed by the junction of three or more cells, passes thence into the interspaces between the cells (Fig. 67), and since these interspaces open into the minute biliary

ducts (Fig. 62, *b, b*), they may be regarded as the beginnings of the latter. The bile-ducts begin then simply as intercellular passages, possessing no proper walls distinct from the cells bounding them.

At the margin of the lobule, however, a basement membrane becomes more evident, and the cells covering it present rather a columnar shape as compared with the polyhedral form of the true hepatic cells. The cellular passages or interspaces having now become true walled ducts, with a diameter of the  $\frac{1}{200}$ th of a mm. ( $\frac{1}{5000}$ th of an inch), ramify between the lobules, and are here seen to consist distinctly of basement membrane lined with columnar epithelium, while the larger ducts, in addition to the basement membrane, possess abundant elastic tissue, and a certain amount of plain muscular tissue.

In addition to the mucous glands opening into the ducts, large racemose cæcal-like glands are present often in such great numbers as almost to conceal the parent tube from which they spring. The use of these glands is not known.

That the bile-ducts begin as just described, is further confirmed by the manner in which the liver develops, and by its structure in the lower animals.

The liver, as we shall see when we come to study the development of the organs of the body, first appears as a bud or diverticulum (Fig. 68, *L*) of that part of the intestine which afterward in the adult becomes the duodenum and, like the latter, consists of two layers, an external intestinal fibrous (*i*), and an internal intestinal glandular (*g*).

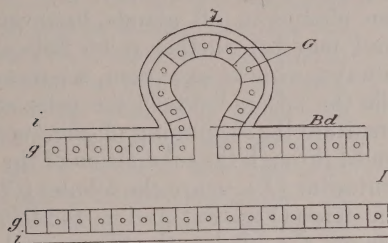
In the former are developed the capillary vessels, which, as we have seen, connect the portal and the hepatic veins; in the latter, the hepatic cells. Very soon the primitive sac-like diverticulum of the intestine subdivides into the two primitive lobes (Fig. 69, *L, L*), while through the narrowing of that part of the sac opening into the intestine (*Bd*) a duct is formed, the primitive bile-duct, a diverticulum from the latter constituting the future gall-bladder. It is evident that in this early

<sup>1</sup> Choezonszczewsky: Virchow's Archiv, 1866, Band xxxv. S. 153.



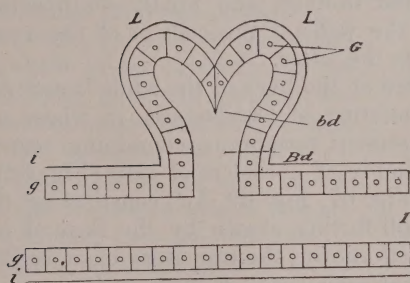
embryonic condition of the liver the intestinal glandular layer (*g*) lining the sac constitutes the secreting portion of the gland, and the interior of the sac (*bd*), the beginning of the bile-duct, since the cavity of the

FIG. 68.



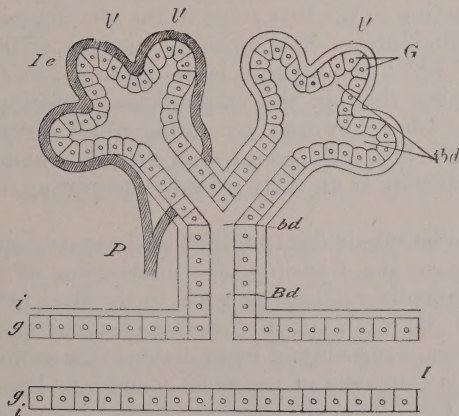
Development of the liver.

FIG. 69.



Development of the liver.

FIG. 70.



Development of the liver.

former (*bd*) is continuous with that of the latter (*Bd*), while the intestinal fibrous wall (*i*) of the sac supports the bloodvessels (Fig. 70, *P*) supplying the blood, out of which the glandular cells (*G*) lining the sac will elaborate the bile. The latter passes thence by the duct (*Bd*) into

the intestine (*I*). The structure of the liver at this stage is therefore similar to that of any other true gland, the simplest expression of which is a basement membrane separating blood on one side from cells on the other, the latter elaborating out of the former the secretion or excretion characteristic of the gland.

Such a disposition obtains in all glands, however complicated the structure of the gland may be, whether it be follicular, tubular, racemose, the cells are always, without exception, separated from the blood by a membrane, while the spaces between the cells ~~and~~ into which the secretion exudes, constitute the beginning of the duct; further, just as the lobes *LL* are formed through the subdivision of the primitive sac-like diverticulum of the intestine (*L*), so are the lobules (*ll*) formed through the subdivision of the lobes (Fig. 70) and as the lobes are defined by the fibrous wall (*i*), so are the lobules, the fibrous wall of the embryonic sac corresponding to Glisson's capsule in the adult, which dipping down between the lobules with the interlobular veins and the hepatic cells becomes thinner and thinner, and finally disappears, or becomes so fused with either the walls of the cells or of the vessels, as to be indistinguishable from the latter.

That the structure of the liver in the adult is essentially the same as in the embryo, consisting of bloodvessels, in whose meshes (Fig. 65) lie cylinders of basement membrane, containing secreting cells, or in the deeper parts simply of cylinders of cells (Fig. 62), the spaces between the latter (Fig. 67, Fig. 69, *bd*) constituting the beginnings of the bile-ducts, is still further shown by the facts of comparative anatomy. For as is well known, the <sup>are/</sup>transitory changes through which the liver of the higher animals passes ~~is~~ <sup>are</sup> more or less permanently retained in those of the lower ones. Thus, in the amphioxus the lowest of vertebrates, the liver consists of a simple sac-like diverticulum of the intestine, corresponding to the first stage in the development of the liver of the higher vertebrates. Passing to the lowest of fishes, the marsipobranchiæ, of which the myxine is an example, we find the liver a little more complex than in the amphioxus, consisting of two lobes with lobules, the lobes, however, remaining quite distinct throughout life, whereas in the higher vertebrates on the other hand they coalesce more or less completely at an early period, constituting in the adult one organ.

8/ The racemose-like, subdivided condition of the embryonic liver, which, as we have just seen, is a transitory one in the liver of the higher vertebrates, is permanently retained as such in the liver of many invertebrates; the liver, for example, in the slug (*Limax*) and snail (*Helix*) among the mollusca, consisting of lobes divided into lobules, each lobule consisting of cæca composed of basement membrane lined with mucous secreting cells. Essentially the same structure obtains in the liver of the lamp shells or brachiopoda (*Terebratulina*), consisting in these animals of numerous cæca lined with cells easily separable from each other, ~~and~~ over which the visceral bloodvessels ramify.

The same type of structure is seen in the liver of the crustacea, consisting in our common crayfish (*Astacus*) of two lobes, one in each side of the intestine, and united by an isthmus, each lobe consisting of long

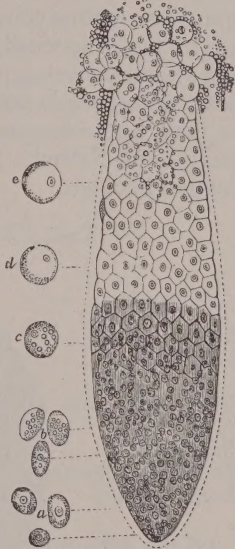


conical caeca massed together, the latter (Fig. 71) consisting of basement membrane, supporting numerous secreting cells, on the inner surface. The same disposition essentially obtains in the liver of the *carripedia*, *carripedia* being well seen in the common barnacle (*Balanus*). It is needless further to multiply examples, since wherever the liver exists in such a condition that its minute structure can be readily made out, it will invariably be found to consist of caeca more or less aggregated together, consisting of basement membrane lined with cells between and around which the bloodvessels ramify, the spaces between the cells constituting the beginning of the bile-ducts. *A priori*, therefore, we should expect to find the minute structure of the liver essentially the same as that of the lower animals, and such we have found to be the case as studied in its minute structure, and in its development.

It is held, however, by many physiologists that the glands which in the invertebrates we have described as being biliary in function, are not really such, the secretion elaborated by them not containing the characteristic bile acids. Even admitting that this is the case, on the supposition that the transitory stages through which the higher animals pass are permanently retained in the lower, one might expect to find the bile in the latter not corresponding exactly in composition with that of the former, but rather with a transitory stage in the development of the same. Further, the fact of the biliary tubules in insects secreting urea, uric acid, etc., so far from being inconsistent with the view of the tubules being biliary in function is confirmatory of it, since, as we shall see hereafter, there are good reasons for supposing that urea, to a certain extent, at least, is produced in the liver of vertebrates.

The bile as obtained by Jacobsen<sup>1</sup> from a case of biliary fistula was clear greenish, brownish-yellow, neutral in reaction, and of a specific gravity of 1.002; when mixed however with mucus, as is the case when taken from the gall-bladder, the bile is more or less ropy in consistence, with an alkaline or neutral reaction, having a faint odor, a bitter taste and a specific gravity of about 1.020, and bright golden-red in color, as is the case also in the bile of the omnivora and carnivora, that of the herbivora being, on the contrary, of a golden or bright green, the difference being due, as we shall see, to the relative amount in which the bile pigments bilirubin and biliverdin are present. It is oxidation of the latter which gives rise to the changes in color which the bile exhibits after exposure.

FIG. 71.



One of the hepatic caeca of *As-tacus affinus* (crayfish), highly magnified, showing the progress of development of the secreting cells, from the blind extremity to the mouth of the follicle: specimens of these, in their successive stages, are shown separately at *a*, *b*, *c*, *d*, *e*. (LEIDY.)

<sup>1</sup> Jahresber, der Thier Chemie, iii. S. 193, 1873. Hermann: Physiologie, Funfter Band, S. 119.

The bile when shaken up with air or water foams up into a frothy mixture. This property is due to the presence of the biliary salts. The bile is also dichroic—that is, it presents two different colors according to its mass, when examined with transmitted light; thus, while a layer of ox bile two or three centimetres thick is green, that of five or six centimetres appears red. The bile is also fluorescent; thus, if green bile be viewed by the violet or blue rays of the spectrum, it becomes faintly luminous, with a yellow, greenish tint.

The bile, chemically, is a highly complex fluid, consisting of water, biliary salts, mucus, pigment, cholesterin, fats, and inorganic salts, the water and solids being in 100 parts in the proportion of about 86 to 14, as may be seen more in detail from Table XXXVIII., giving the analyses of Frerichs and Gorup Besanez<sup>1</sup> of human bile obtained from the gall-bladder.

TABLE XXXVIII.—COMPOSITION OF THE BILE.

| In 100 parts.             | Frerichs.       |                 |                 | Gorup Besanez.  |                   |                 |
|---------------------------|-----------------|-----------------|-----------------|-----------------|-------------------|-----------------|
|                           | Man,<br>æt. 18. | Man,<br>æt. 22. | Man,<br>æt. 49. | Man,<br>æt. 68. | Woman,<br>æt. 28. | Boy,<br>æt. 12. |
| Water . . . . .           | 86.00           | 85.92           | 82.27           | 90.87           | 89.81             | 82.81           |
| Solids . . . . .          | 14.00           | 14.08           | 17.73           | 9.13            | 10.19             | 17.19           |
|                           |                 |                 |                 |                 | 5.65              |                 |
| Biliary acids with alkali | 7.22            | 9.14            | 10.79           | 7.37            | ....              | 14.80           |
| Fat . . . . .             | 0.32            | 0.92            | 4.73            | ....            | 3.09              |                 |
| Cholesterin . . . .       | 0.16            | 0.26            |                 |                 |                   |                 |
| Mucus and pigment .       | 2.66            | 2.98            | 2.21            | 1.76            | 1.45              | 2.39            |
| Inorganic salts . .       | 0.65            | 0.77            | 1.08            | ....            | 0.63              |                 |

Of the different principles which constitute the bile, most of them, as the water, cholesterin, fat, and inorganic salts, preëxist as such in the blood, and are simply eliminated from the latter by the liver cells; the biliary salts and the biliary pigment, however, are not found in the blood, but are elaborated by the liver cells out of the principles brought to them by the blood. The presence of the biliary acids, then, in the urine, for example, is a proof that the bile has been secreted, but has been prevented by some obstruction from passing into the duodenum and being reabsorbed. A jaundice from mere obstruction in which, however, the bile has been secreted, can be then distinguished from one in which no bile has been secreted by the presence or absence of the biliary acids in the urine; the color of the skin in the latter case being probably due to the diffusion into the tissues of the broken-down hæmoglobin of the red blood-corpuscles, and which we shall see is almost identical, if not absolutely so, in chemical composition with the biliary pigment.

The biliary salts do not consist, as one would suppose from their name, of simply inorganic salts, such as are ordinarily found in the secretions, but of soda, united with glycocholic and taurocholic acids, the organic nitrogenized acids so characteristic of the bile, and upon which, to a great extent, the properties of the latter depend.

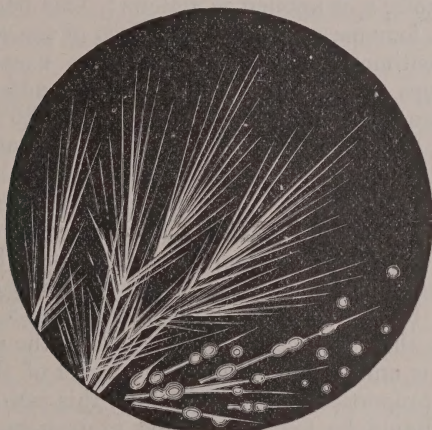
The biliary salts, the sodium taurocholate,  $C_{26}H_{44}NSO_7Na$ , and the sodium glycocholate,  $C_{26}H_{42}NO_6Na$ , may be obtained from the bile in the

<sup>1</sup> Lehrbuch der Physiologischen Chemie, S. 519. Braunschweig, 1878.



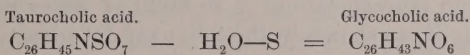
following manner: The bile having been mixed with animal charcoal to decolorize it, is evaporated to dryness, and then treated with alcohol. The alcohol having been distilled off, the dry residue is then further treated with absolute alcohol; anhydrous ether, after filtering, is added to the filtrate until the precipitate formed ceases to be thrown down. After standing some hours the precipitate crystallizes as the resinous matter of the bile, also known as bilin, and which contains both sodium taurocholate and glycocholate, if both biliary acids be present in the bile, and which can be separated from each other by making an aqueous solution of the bilin, adding neutral lead acetate and then filtering. The filtered solution will contain the sodium taurocholate alone, the sodium glycocholate being decomposed and precipitated as an insoluble lead glycocholate.

FIG. 72.



Sodium glycocholate from ox-bile, after two days' crystallization. At the lower part of the figure the crystals are melting into drops, from the evaporation of the ether and absorption of moisture. (DALTON.)

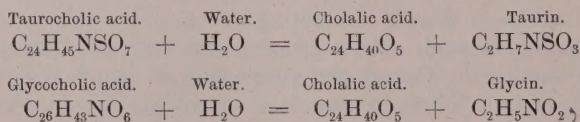
The biliary acids themselves may then be separated from their respective salts by means of dilute sulphuric acid or lead acetate and sulphydric acid. The relation existing, chemically, between these two acids, is shown in the formula:



by which it is seen that, in deducting water and sulphur, taurocholic becomes glycocholic acid. As a general rule, both the biliary salts are present in human bile, though the proportion in which they exist may vary considerably. Thus, in the case of biliary fistula observed by Jacobsen, already referred to, the sodium taurocholate was present only in small quantity or absent altogether. Usually, in the bile of the herbivora the sodium glycocholate preponderates, in that of the carnivora the taurocholate. In the bile of the cat and dog, however, the sodium taurocholate alone is found.

Both the biliary salts crystallize in hemispherical or star-shaped masses of fine radiating needles (Fig. 72) which, while soluble in alcohol and water, are insoluble in ether. The two salts are distinguished from each other, as just mentioned in speaking of the manner of obtaining them, in that the sodium taurocholate is not precipitated by the neutral lead acetate,  $\text{Pb}(\text{C}_2\text{H}_3\text{O}_2)_2 \cdot 3\text{Aq}$ , but only by the tribasic lead acetate,  $\text{Pb}(\text{C}_2\text{H}_3\text{O}_2)_2 \cdot 2\text{PbO}$ . It is an interesting fact that the biliary salts, like glucose, lactose, and glycogen, exert a right-handed rotation on polarized light, all other substances in the animal body, so far as is known, having the opposite effect when examined by polarized light. The play of colors from cherry-red to purple or violet ensuing when cane sugar and sulphuric acid are added to bile, or to a solution containing the biliary salts or acids, and which is due to the decomposition of the latter, or to the cholalic acid entering into their formation, furnishes a very simple but reliable test for bile. This test, commonly known as Pettenkofer's, is applied as follows: One part of cane sugar being dissolved in four parts of water, one drop of the solution is added to every cubic centimetre of the solution to be examined. To this mixture a few drops of sulphuric acid are slowly added, the temperature of the mixture not being allowed to rise above  $70^\circ$  Cent. If bile acids be present in proportions of 1 to 500 in a solution treated this way, a cherry-red color first appears, which rapidly changes to violet, and then to a deep red purple. Inasmuch, however, as there are other substances, such as albuminous matters, amylic alcohol, olein, morphine, codeine, etc., which present this same play of colors when treated with cane sugar and sulphuric acid, it is necessary to point out the precautions which must be taken in applying Pettenkofer's test for bile, in order to exclude these sources of error. With the exception of the morphine, which is unlikely to occur in an extract of the animal fluid, especially in the proportions just referred to, this can be accomplished if the suspected liquid be first evaporated to dryness, the dry residue extracted with absolute alcohol and decolorized, if necessary, with animal charcoal, then precipitated with ether, and the precipitate dissolved in water. Spectrum analysis of Pettenkofer's test can also be used in distinguishing bile from the substances just referred to, and which give the same reactions.

Pettenkofer's test, when carefully applied, is an extremely delicate one, since a solution of sodium glycocholate in the proportion of 1 to 2000, and sodium taurocholate of 1 to 3000 of water respectively, can be recognized by it; as shown in the following formula;



—Glycocholic acid, when boiled with dilute sulphuric or hydrochloric acid, caustic potash, or baryta water, becomes cholalic acid and glycin, and in a similar manner taurocholic acid can be shown to consist of the same acid and taurin. While cholalic acid is a non-nitrogenized acid,



as may be seen in both the above instances, it is associated with a nitrogenous body, in the first case with glycine (amido-acetic acid), and in the second with taurine (amido-isethionic acid). The reaction given in the above formula is as interesting from a pathological as from a purely chemical point of view, since, in all probability, as shown by Hoppe-Seyler,<sup>1</sup> the decomposition of glycocholic and taurocholic acids into cholic acid, glycine, and taurine takes place in the intestines, the acid passing out of the body in the feces, the ammonium compounds, the glycine and taurine, being reabsorbed. The view of the biliary acids being decomposed in the intestine and partially absorbed, or entirely so undecomposed, is confirmed by several facts. Thus, in experimenting with a dog, whose bile usually furnished in five days 2.274 grammes (34 grains) of sulphur, Bidder and Schmidt<sup>2</sup> found in the feces during that period 0.384 of a gramme (4.6 grains), of which about 0.154 gramme (1.5 grain) could have been derived from the bile, the remaining sulphur being obtained from the hair in the feces. That is, only a fractional part of the sulphur originally present in the bile was found in the feces, whereas had not the taurocholic acid been decomposed and partly absorbed all of the sulphur would have been found there. On the other hand, that the biliary acids may be absorbed undecomposed is shown by the observations of Taffeiner,<sup>3</sup> who found the biliary salts in chyle from the thoracic duct. Further, the experiments of Schiff,<sup>4</sup> in which it was shown that the amount of bile evacuated through a biliary fistula was about one-third of that normally poured into the intestine, would lead one naturally to suppose that the bile is ordinarily absorbed in part, at least, soon after it has passed into the latter.

The color of the bile, as we have already mentioned, depends upon the proportion in which the bile pigments, bilirubin and biliverdin, are present. Bilirubin,  $C_{16}H_{18}N_2O_3$ , the red or orange-red coloring matter of the bile, can be obtained from gall-stones by extraction, is crystallizable, readily soluble in alkaline liquids and chloroform, less so in alcohol and ether, but entirely insoluble in pure water. If to a solution of bilirubin, spread out on the surface of a porcelain plate, for example, a drop of nitroso-nitric acid be added, a characteristic play of colors—green, blue, violet, red, and, finally, yellow—will be observed at the circumference of the drop of acid as it diffuses itself through the solution, and which is due to the successive oxidation of the bilirubin. This reaction is an exceedingly delicate one, the play of colors being evident in solutions of bilirubin containing only 1 part in 70,000, and is, therefore, utilized as Gmelin's test in determining the presence of the coloring matter of the bile. That bilirubin, though not identical, is at least the modified coloring matter of the red blood-corpuscles or hæmoglobin, appears to be shown from the fact of its being found in old blood extravasations, on account of its similarity in color and chemical composition with that of the latter, and that if the blood freshly drawn, and alternately frozen and thawed, be reinjected into

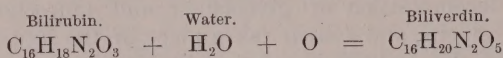
<sup>1</sup> Virchow's Archiv, Band xxv. S. 181; xxvi. S. 519.

<sup>2</sup> Die Verdauungssäfte, S. 217. Leipzig, 1852.

<sup>3</sup> Sitzungsberichte, Band lxxvii. S. 286. Wien, 1878.

<sup>4</sup> Pflüger's Archiv, 1870, S. 598.

the circulation, bilirubin is found in the urine. Bilirubin, when oxidized, loses its red color, becoming green, as in the first stage of Gmelin's test, and is then transformed into biliverdin, the green colored pigment of the bile, the process being apparently one of hydration as well as of oxidation, as shown by the following formula :

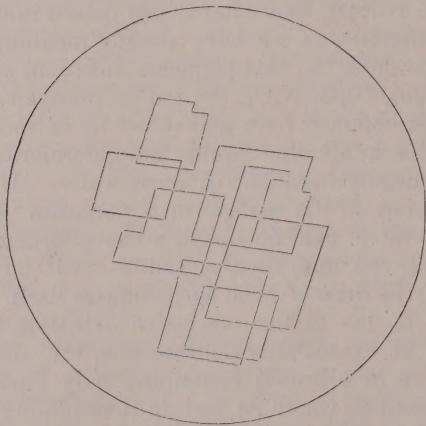


Biliverdin crystallizes somewhat imperfectly from an evaporated solution in glacial acetic acid, is insoluble in water, ether, and chloroform, but is readily soluble in alkaline solutions and alcohol. It frequently constitutes an ingredient of human gall-stones. Its presence can not only be determined by Gmelin's test, but by means of spectrum analysis.

Both bilirubin and biliverdin pass as the coloring matter of the bile into the alimentary canal, in the lower part of which, as we shall see presently, they give the feces their characteristic color, and as such pass out of the body.

Cholesterin,  $\text{C}_{26}\text{H}_{44}\text{O}$ , so called on account of its having been first obtained as a solid deposit from the bile, is a constant ingredient of that fluid, though occurring only in the proportion of one per cent. It is a non-nitrogenous, crystallizable body, appearing as thin, colorless, transparent, rhomboidal plates (Fig 73) when deposited from its ethereal or

FIG 73.



Cholesterin, from an encysted tumor. (DALTON.)

alcoholic solution. It is insoluble in water, but soluble in a solution of the biliary salts, oily liquids, and chloroform, as well as in ether and boiling alcohol.

Cholesterin is found in the blood, spleen, crystalline lens, brain, spinal cord, and nerves, as also in other parts of the body. It differs, therefore, from the biliary salts and pigment in not, like them, being elaborated in the liver, but as preëxisting in the tissues, and being simply separated from the blood by that organ and eliminated from the system as part of



the bile, passing out of the body in the feces as cholesterin, or, according to Flint,<sup>1</sup> as stercorin, a modified form of the same.

Of the remaining principles entering usually into the composition of the bile a few words will suffice. According to Jacobsen, the bile obtained from the biliary fistula already referred to, contained, in addition to biliary salts, pigment and cholesterin; fractional quantities of free fat, lecithin, and sodium palmitate and stearate. Of the mineral salts present, sodium and potassium chloride, sodium and calcium phosphate, and sodium carbonate, the sodium chloride and sodium phosphate were most abundant, the former being in the proportion of 5.4 parts, the latter 1.3 per thousand.

We have seen that the bile is both a secretion and an excretion—that is, that it contains some principle which fulfils some function, in all probability that of promoting digestion and absorption, and some principle which, if retained within the system, proves excrementitious, and that the biliary salts are, to a great extent, reabsorbed, while the pigment and cholesterin pass out of the body in the feces either as such or more or less modified. The natural conclusion from these facts seems to be that the quality of the bile as a secretion is due to its biliary salts, and as an excretion to its biliary pigment and the cholesterin.

From what has been said of the manner in which the saliva, gastric and pancreatic juices are secreted, it might be supposed that the bile is elaborated by the liver cells in a somewhat similar manner out of materials brought to them by the blood. That such is the case, appears from the fact already mentioned of the bile not preëxisting as such in the blood, and further of it not accumulating in the blood during the short period which some animals, frogs, for example, live after extirpation of the liver.

That the bile is not a mere filtrate from the blood is shown, as in the case of the secretion of the saliva, from the pressure under which it is secreted (in the dog 220 mm. (8.8 in.) sodium carbonate solution<sup>2</sup>) being greater than that of the blood supplying the liver, and that chemical action is going on during secretion is equally evident from the amount of heat developed and carbonic acid produced.

That there is some genetic connection between the hæmoglobin of the blood, and the bilirubin and biliverdin of the bile, after what has been said of the latter substances there can be little doubt, and that the cholesterin, taurin, and glycin of the tissues as well as such amounts of the latter substances as are reabsorbed from the intestine may be carried to the liver cells and elaborated synthetically into bile, the latter to a certain extent, therefore, being made over again out of the same elements, appears probable. It must be admitted, nevertheless, that the materials out of, and the manner in which the bile is exactly secreted or excreted is still of a very speculative nature.

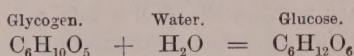
The function of the liver, as might be supposed from its size and constant presence in the animal kingdom, is not however limited to the secreting or excreting of bile, for, as we shall see, it exercises an impor-

<sup>1</sup> Physiology, 1867, vol. ii. p. 299.

<sup>2</sup> Heidenhain: Hermann's Physiologie, Funfter Band, S. 269.

tant influence certainly in the embryo, and very probably also in the adult, in the elaboration of the red blood-corpuscles. Further, the liver cells have the power of developing, storing up, and transforming a substance glycogen; so called, from the resemblance to and readiness with which it becomes sugar, and the origin and use of which may be considered as appropriately here as elsewhere, though it should be mentioned that glycogen is found in the brain, muscles, placenta, and other parts of the body as well as in the liver.

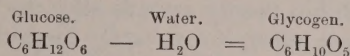
Glycogen,  $C_6H_{10}O_5$ , a white pulverulent mass, is isomeric with starch and dextrin. It differs however, physically from the latter in that its solution is opalescent, while that of dextrin is clear, and that the addition of iodine gives to the solution of glycogen a deep brownish-red color, but to that of dextrin a rosy red, and to starch the characteristic blue. Glycogen is soluble in both hot and cold water, but insoluble in ether and alcohol, and is one of the few substances in the animal body that deviate the plane of polarization to the right. Glycogen in solution, like other starchy bodies, is readily converted into glucose when boiled, for example, with a dilute mineral acid, or brought in contact at the temperature of the body with saliva, pancreatic or intestinal juice, or serum. Glycogen becomes glucose also, if simply allowed to remain in the liver after death, or if brought in contact with its tissue after removal from the body, the albuminous principles of the liver very probably assisting as ferments in the development, though the phenomenon is essentially one of hydration as shown by the formula :



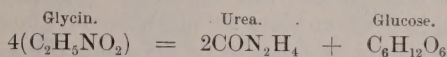
Glycogen can be readily obtained in the following manner. Immediately after death, the liver of a well fed animal is taken out of the body and cut up into small pieces, and coagulated with boiling water. A concentrated decoction is then made of the liver tissue thoroughly ground up, and decolorized with animal charcoal. Strong alcohol being now added, the glycogen will be precipitated as a white powder; but this is impure, being mixed with a small quantity of glucose, biliary salts, and albuminous matter. The latter can be removed, however, by washing with alcohol, and boiling with potassium hydrate. The residue being filtered and dissolved in water, and any albuminous principles still present being removed with acetic acid, the glycogen is reprecipitated with alcohol, and then dried, when it can be kept for a long time, it retaining its properties indefinitely. The quantity of glycogen in the liver varies, as a general rule, between seven and seventeen per cent.—that is to say, assuming that the liver in man weighs about fifty ounces, the amount of the glycogen present would be from three to eight ounces, the amount depending, however, upon the length of time elapsing since the taking of food, and the character of the latter, increasing with digestion and diminishing with fasting, and disappearing altogether if no food be taken for four or five days, being more abundant on a vegetable than on an animal diet, and particularly abundant if the food consists largely of carbohydrate matter. When the chemical composition of glucose and glycogen is compared, and when it is remem-



bered that all of the starch and sugar of the food is transformed into glucose during digestion, the above becomes intelligible, on the supposition that the glucose carried by the portal vein to the liver during absorption is converted by and stored up in the liver cells as glycogen, the transformation of the glucose into glycogen being one of dehydration, as shown by the formula :



The fact of glycogen being developed on an animal diet as well as on a vegetable one, though in less amount, so far from being an objection to the origin of glycogen, as just offered, is a confirmation of it, since it is readily conceivable how nitrogenized matter may, like glycin, split up in the economy into glucose and urea, as shown by the formula :



the glucose becoming then glycogen, as in the former case, where it was derived from vegetable matter, and the urea being eliminated by the kidneys. That such a transformation of nitrogenized matter actually takes place in the system, at least under certain conditions, appears from the fact that in certain cases of diabetes,<sup>1</sup> when the food contained no carbohydrate matter, the glucose increased *pari passu* with the urea. The above, to a certain extent theoretical considerations, are confirmed by experimental ones. Thus it has been shown by Bernard,<sup>2</sup> Pavy,<sup>3</sup> Doch,<sup>4</sup> Tscherinow,<sup>5</sup> and others that the amount of glycogen in the liver is notably increased within a few hours after the taking of starchy or saccharine articles of food, and that while glycogen is developed on an animal diet, the amount produced is far less than on a vegetable one.

There appears to be no doubt, therefore, that the carbohydrate principles of the food, and to some extent the nitrogenized ones also, transformed into glucose, together with the glucose from the glycin of the glycocholic acid, are conveyed in the blood of the portal vein to the liver, and that the glucose so derived is, probably by dehydration, converted into glycogen, and, for the time being, at least, is stored up as such in the liver cells. That the glycogen remains, however, only temporarily in the liver, appears from the fact, as shown first by Bernard,<sup>6</sup> that in a fasting animal, or in one that has been fed on an exclusively meat diet, ~~that~~ the liver and the blood of the hepatic vein contain glucose, though there is not the slightest trace of it in that of the portal vein, the glycogen stored up in the liver during the intervals of digestion being gradually converted into glucose, and conveyed away by the hepatic veins into the general circulation.

That the transformation of glycogen into glucose is merely a question of time, is shown by the fact that a decoction made out of a liver taken

<sup>1</sup> Singer : Med. Chir. Trans., xliii. p. 327.

<sup>2</sup> Physiologie Experimentale, p. 159. Paris, 1855.

<sup>3</sup> Nature and Treatment of Diabetes. London, 1862.

<sup>4</sup> Pflüger's Archiv, 1872, Band v. S. 571.

<sup>5</sup> Virchow's Archiv, 1869, Band xlvii. S. 102.

<sup>6</sup> Op. cit., p. 204.

out of the body of a fasting animal, is clear, whereas if it is made out of one taken from an animal fed within a few hours, it is decidedly opalescent through the glycogen it contains not as yet having been transformed into glucose.

It is denied by some experimenters that the liver actually contains glucose during life. Inasmuch, however, as glucose can be demonstrated in the liver within twenty seconds after the death of the animal from which it has been taken, it can hardly be doubted that such is the case. While there may be a difference of opinion as to whether the liver contains glucose during life, there is no difference of opinion as to its containing glucose after death. Indeed, if all the blood be washed out of the liver by forcing water through the portal vein, the liquid, as it escapes by the hepatic vein, will be found to contain glucose, and this even after upward of half an hour after repeated injections. And then, when the presence of glucose can no longer be demonstrated, if the liver be put aside in a warm place for a few hours, glucose can again be obtained, it being a long time before its glycogen, the source of the glucose, is exhausted.

As to what becomes of the glucose thus constantly poured into the general circulation from the liver, there can be no doubt of it being ultimately transformed, probably through oxidation, into carbonic acid and water. Just how and where this final change is brought about, is still not exactly known, but in all probability the change is effected in the tissues, since, as we shall see, the venous blood contains less glucose and more carbonic acid than the arterial.

In conclusion, it may be pointed out that the transformation of glucose into glycogen, and of glycogen into glucose in the animal, finds an analogy in the vegetable, since, as is well known, the starch in the leaves of a plant having been converted into sugar, passes down to the roots, where not infrequently it is reconverted into starch.

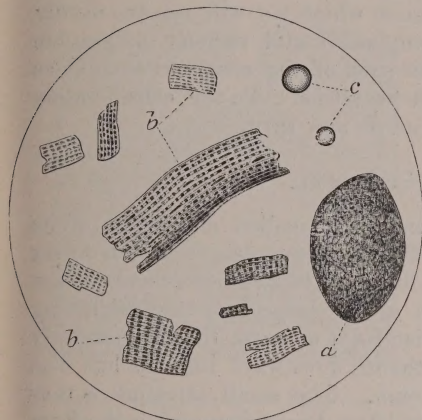
While for convenience' sake we have studied separately the different effects of the intestinal, pancreatic, and biliary secretions, it must not be forgotten that the action of these secretions in digestion is simultaneous, and <sup>that</sup> their actions are, to a certain extent, supplementary to those produced by the saliva and gastric juice. Whenever, therefore, the opportunity presents itself of opening the alimentary canal of a human being who has died in full digestion, it will be well to take advantage of it, with reference to the examination of the changes which the food undergoes, through its successive admixture with the saliva and the gastric juice, and its further modifications due to the simultaneous action of the intestinal secretions. Essentially the same result can be obtained, experimentally, so far as the digestion of meat or vegetable food is concerned, by killing dogs or rabbits respectively, at different periods after feeding, and examining the contents of the stomach or intestine microscopically.

Figs. 74, 75, and 76 give an excellent idea of the general appearance exhibited by meat and fat, according to the part of the alimentary canal of the dog examined, from which the specimen was taken. Thus (Fig. 74) in the grayish grumous acid fluid of the stomach are seen under the microscope more or less disintegrated muscular fibres, fat vesicles,



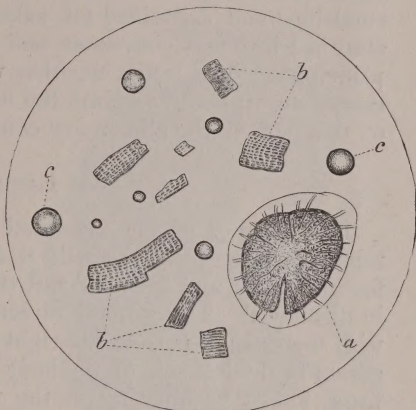
and a few oil globules. In the duodenum (Fig. 75) the muscular fibres are pale, broken up, further disintegrated, though still recognizable by their striæ. The fat vesicles become shrivelled, the oil drops are

FIG. 74.



Contents of stomach during digestion of meat, from the dog. *a*. Fat vesicle, filled with opaque, solid, granular fat. *b, b*. Bits of partially disintegrated muscular fibre. *c*. Oil globules. (DALTON.)

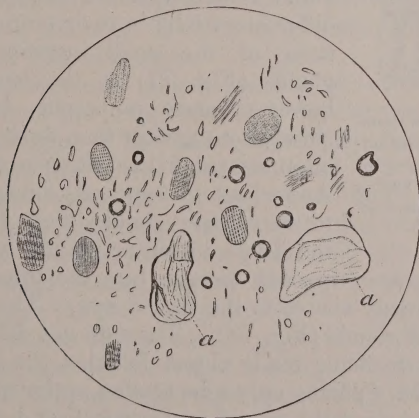
FIG. 75.



From duodenum of dog, during digestion of meat. *a*. Fat vesicle, with its contents diminishing. The vesicle is beginning to shrivel and the fat breaking up. *b, b*. Disintegrated muscular fibre. *c, c*. Oil globules. (DALTON.)

increased in number, and the fat is, to a great extent, liquefied and emulsified. In the middle and lower parts of the small intestine (Fig. 76) the meat is seen to be entirely broken down, a considerable quantity of granular débris is present, the fat vesicles are found empty, while

FIG. 76.



From last quarter of small intestine. *a, a*. Fat vesicle, quite empty and shrivelled. (DALTON.)

the emulsified fat has almost disappeared, having been taken up by the absorbents.

The chemical changes produced in the food by digestion, are of the

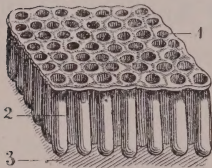
same continuous character. The starches gradually become glucose, the albuminous substances are converted into albuminose, leucin, and tyrosin, while the fats are emulsified, and probably, to a certain extent, also saponified. Thus, during intestinal digestion we find the alimentary canal containing a mixture consisting of albuminose, glucose, and emulsified and saponified fat, substances which we will see are readily absorbed by the bloodvessels and lymphatics, and various indigestible principles. The latter, together with such of the above substances as escape absorption, pass into the large intestine. To the consideration of this part of the alimentary canal let us now turn.

### THE LARGE INTESTINE.

This portion of the intestinal canal is so called on account of its relatively large size. Usually it is found to measure from four to six feet in length, and from one and two-thirds to two and two-thirds inches in diameter.<sup>1</sup> The general direction of the large intestine beginning with the cæcum, is from the right iliac fossa upward, then transversely across to the left side of the body; thence downward into the left iliac fossa, finally terminating as the rectum. The small intestine is thus surrounded by the large intestine, the latter being disposed in the form of a horseshoe.

The large intestine, like the small, consists essentially of two coats, a mucous, including the submucous, and a muscular. In addition, the large intestine is, to a great extent, covered with peritoneum, which serves to maintain it in position, and to connect it with

FIG. 77.



Section of the mucous membrane of the colon. 1. Free surface exhibiting the orifices of the tubular glands. 2. 3. Fibrous tissue moderately magnified. (LEIDY.)

certain of the abdominal and pelvic viscera. While the villi and valvulæ conniventes are absent in the large intestine, throughout the whole extent of its mucous membrane there are found tubular and solitary glands which do not differ essentially in their minute structure from those of the small intestine. The tubular glands (Fig. 77) of the large intestine are, however, more numerous, longer and more closely set together than those of the latter, and often are subdivided at their cæcal extremities. According to some physiologists,<sup>2</sup> in addition to the solitary glands, there are also found in the large intestine glands which differ from

these in that they are supposed to open into the intestine by an aperture said to be plainly visible to the naked eye. These glands are the so-called utricular glands (Fig. 78). They do not differ from the ordinary solitary glands, being really closed follicles, the so-called aperture or opening (Fig. 78, *f*) being only a depression in that part of the mucous membrane situated over the gland and separating it from the interior of the intestine.<sup>3</sup>

<sup>1</sup> Cyclopædia of Anatomy and Physiology, v. p. 362.

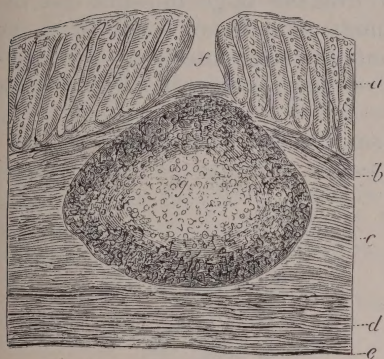
<sup>2</sup> Milne Edwards: Physiologie, 1860, tome vi. p. 408.

<sup>3</sup> Sappey: Anatomie, 1879, tome iv. p. 257. Kolliker: Gewebelehre, 1867, S. 422. Hyrtl: Anatomie, 1880, Fünfzehnte Auf. S. 689. Henle: Anatomie, 1873, Zweiter Band, S. 193. Quain's Anatomy, 1878, vol. ii. p. 3.



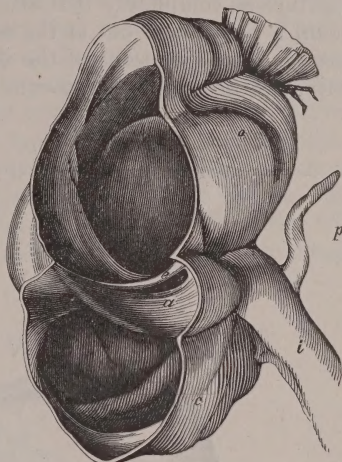
The mucous membrane of the large intestine is paler, thicker, and more closely adherent to the underlying parts than that of the small intestine. The muscular coat of the large intestine differs considerably

FIG. 78.



Section of large intestine showing utricular gland. *f.* Depression in mucous membrane. *a.* Tubular glands. *b.* Muscularis mucosæ. *c.* Submucous coat. *d.* *e.* Muscular coats. (KOLLIKER.)

FIG. 79.



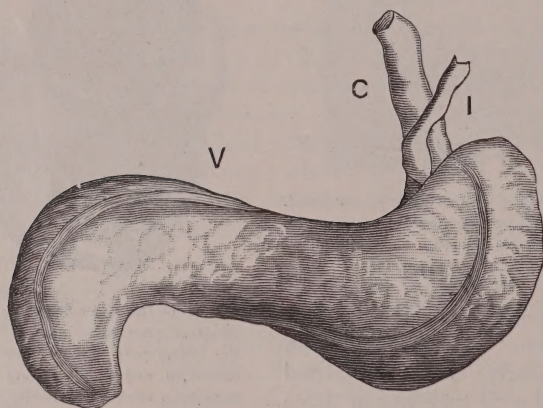
View of the ileo-colic valve from the large intestine (after Santorini).  $\frac{1}{2}$  The figure shows the lowest part of the ileum, *i*, joining the caecum, *c*, and the ascending colon, *o*, which have been opened anteriorly, so as to display the ileo-colic valve; *a*, the lower, and *e*, the upper segment of the valve. *p.* Vermiform appendix.

in certain points from that of the small intestine. Thus, in the colon more particularly, the longitudinal fibres are gathered together in three well-marked bands, one of which is anterior, while the other two are latero-posteriorly situated. The large intestine is divided by anatomists into three portions, the caecum, colon, and rectum, these differing in their size, shape, and the character of their mucous and muscular coats.

The most important part, physiologically, of the caecum or caput coli, the widest portion of the large intestine, is the ileo-caecal valve, by means of which the contents of the ileum, after they have passed into the large intestine, are prevented from returning into the small intestine. The small intestine opens into the large intestine by a slit-like aperture (Fig. 79, *a e*) which lies nearly transverse to the direction of the latter. This aperture is bounded above and below by two semilunar folds or valves which project inward toward the caecum and colon. At each end of the aperture the two valves or folds run into each other and are then prolonged at each side as a ridge or frænum, which gradually fades away. That portion of the valve which looks toward the ileum is covered with villi, and in other respects resembles the mucous membrane of the small intestine, while that upon the opposite side of the valve is destitute of villi, and its mucous membrane is like that of the large intestine. Each segment of the valve is covered with mucous membrane, and consists of submucous tissue and muscular fibres, derived from the circular muscular fibres of both the ileum and large intestine.

The longitudinal muscular fibres of the ileum, however, run continuously into those of the large intestine, taking no part in the formation of the valve, but are stretched across it. The effect of distention of the cæcum by its contents is that the fræna being put on the stretch, the edges of the valves are brought in apposition, closing the ileo-cæcal aperture so completely that all reflux from the large intestine into the ileum is prevented, but at the same time no hindrance is offered to the passage of the contents of the ileum into the large intestine. An interesting feature about the cæcum is its vermiform appendix (Fig. 80, V),

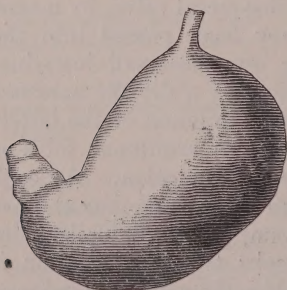
FIG. 80.



Cæcum of capybara. (From nature.)

a worm-like tube, beginning at its lower end and terminating in a blind extremity, attaining usually about a length of from three to six inches, and having a diameter about the size of a quill.

FIG. 81.



Stomach of capybara. (From nature.)

The vermiform appendix, so far as is known, has no use in man, but is a very interesting structure as representing in man, in a rudimentary condition, that which is well developed and performs important functions in many animals. Thus in the horse, tapir, elephant, rabbit, and beaver the cæcum is very large; in the capybara (*hydrochoerus*), a species of rodent, the cæcum (Fig. 80) measured twenty-six inches in length, while in a koala (*phascogale*), a small marsupial, also examined by the author, it attained a length of fifty inches. Now, by comparing the cæcum in the capybara with

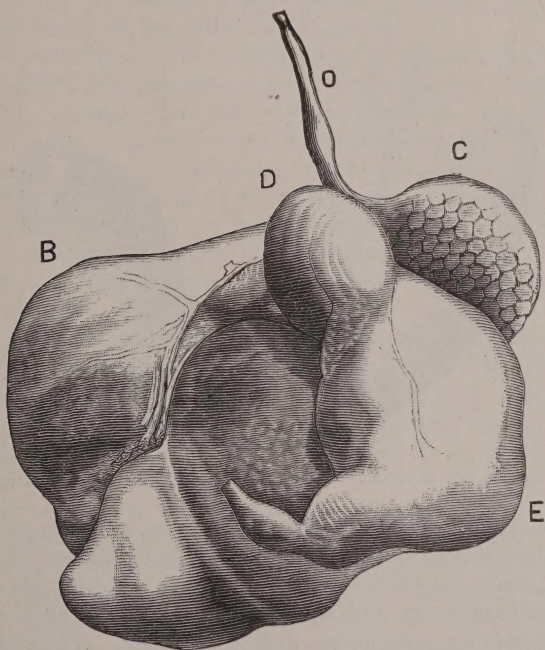
the vermiform appendix in man, it will be found that the latter corresponds to the blind part of the cæcum, V, in the capybara, while the cæcum, or caput coli, in man is homologous with that part of the cæcum in the capybara communicating with the large intestine, I. In other



words, the cæcum in the animals just mentioned is equal in man to the vermiform appendix and cæcum. Further, it will be observed that the cæcum of the capybara (Fig. 80) is much longer than the stomach of that animal (Fig. 81), the latter measuring only ten inches, while it is needless to state that just the reverse relation obtains as regards the same parts in man. The significance of this contrast is evident enough when the digestion of food in man and the capybara is considered. In the first instance, as we have seen, the action of the stomach is very important; in the latter instance it is but relatively so, the imperfect digestion of food in the stomach of the capybara being completed in its cæcum.

In the same manner the cæcum in the tapir, horse, and elephant, etc., supplements the imperfect digestive action of the stomach in these animals. On the other hand, in the giraffe, in which there are four well-developed stomachs, B, C, D, E, (Fig. 82) the cæcum, V, (Fig. 83) is relatively small. In a word, there is an inverse ratio, both anatomi-

FIG. 82.



Stomach of giraffe. (From nature.) O. (Esophagus. B. Rumen. C. Reticulum. D. Psalterium. E. Abomasum.

cally and physiologically, between the stomach and the cæcum; when the one is large and active, the other is small and inactive, and *vice versa*. The conclusion must not, however, be drawn that the cæcum in these animals secretes a gastric, or any other digestive juice. The cæcum rather appears to be a receptacle where the fluids absorbed by the food in its rapid passage through the alimentary canal have time to produce their digestive effects.

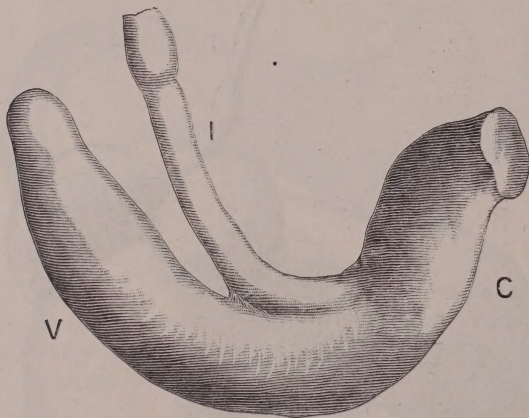
The acid reaction often noticed in the cæcum of animals, and some-

times in man, is not due to acid secretion, but to a kind of lactic or butyric acid fermentation set up in the food, the normal reaction of the secretion of the cæcum being alkaline. That the vermiform appendix in man is a rudimentary organ is confirmed by the fact that it is relatively longer in the embryo than the adult. It is worthy of note that the vermiform appendix is found as in man in all four anthropoid apes, the gorilla, chimpanzee, orang, and gibbon; and more remarkable still that it is present in a marsupial, the wombat (*Phascolomys*).

In addition to what has already been said of the colon, an important feature is, its sigmoid flexure, so called from the S-like curve the colon makes just before passing into the rectum. This curvature, as we shall see, is the position where the feces are temporarily retained.

The large intestine terminates in the rectum, which, while straight in animals in which it was originally described, is far from being such in man. In fact, the rectum in man first passes obliquely downward from left to right, from opposite the left sacro-iliac articulation to the middle

FIG. 83.



Cæcum, etc., of giraffe. V. Cæcum. I. Small intestine. C. Colon.

line of the sacrum. It then curves forward back of the prostate in the male, and the vagina in the female, and finally passes backward and downward, terminating in the anus. The anus is a dilatable orifice, lined with mucous membrane and covered with skin, the skin and mucous membrane becoming continuous with each other. The margin of the anus and lower part of the rectum are embraced by the external and internal sphincter muscles, the levatores ani and coccygei. These muscles serve to support the bowel, and to close its anal orifice. The internal sphincter muscle consists of the circular fibres only greatly developed. It is situated an inch above the anus, extending over about half an inch of the intestine, and is two lines thick.

The rectum, about eight inches in length, is not sacculated like the rest of the large intestine, the longitudinal muscular fibres being scattered over its surface. While the upper part of the rectum is narrow, at the lower part it is dilated into a kind of reservoir just above the



anus. The mucous membrane of the rectum is more vascular, thicker, and redder than that of the colon, and moves more freely over the muscular coat. It is thrown into numerous folds, most of which are however effaced when the rectum is distended.

THE CONTENTS OF THE LARGE INTESTINE.—While there is no reason to suppose that anything like true digestion takes place in the large intestine of man, various important changes are effected there by which the undigested residue of the food is gradually transformed into the feces, the most marked changes being in the consistence, color, and odor of the contents of the large intestine, and which are gradually developed in the undigested food as it passes from the cæcum through the colon into the rectum. As the undigested food passes through the large intestine its liquid portions are being constantly absorbed, the feces therefore have a much firmer consistence than the contents of the ileum. The large intestine is therefore physiologically important, as presenting an extensive absorbing, if not a digestive surface. The absorbing power of the rectum is well known. Indeed, life can be sustained for months by giving nutritious enemata.

The color of the feces is of a dark yellowish-brown, and appears to be due to modified bile pigment, which is precipitated when the acid contents of the stomach or the chyme mix with the bile in the duodenum. As the soda of the bile, on which the solubility of the bile pigment depends, is soon neutralized by the acid gastric juice, the bile pigment is thus set free, and is so modified as it passes through the alimentary canal that ultimately it does not respond to the usual tests. It is well known that when the bile is deficient or absent, the stools become lighter or clay-colored. The color of the feces varies also according to the diet.

While the cause of the odor of the feces cannot be said to be exactly understood, there can be no doubt that it is due to a great extent to the imperfect oxidation of the food, to the presence of skatol ( $C_9H_9N$ ) and indol ( $C_8H_7N$ ), nitrogenous substances developed during pancreatic digestion, to the decomposition of the bile, and to the secretion of the glands of the colon and rectum.

The reaction of the feces is variable, sometimes acid, often alkaline or neutral, depending chiefly upon the kind of food eaten.

The entire quantity of feces passed in twenty-four hours varies from four to seven ounces; as might be expected, there being a greater amount of feces on a vegetable than on an animal diet, the former containing a greater quantity of indigestible matter than the latter. When the contents of the large intestine are examined microscopically, there will be found a number of undigested substances derived from the vegetable and animal foods. Among other matters, the spiral vessels of vegetables, the cortex of grains, hard vegetable seeds, structures generally consisting largely of cellulose, muscular tissue in various stages of disintegration, tendinous and elastic structure, the organic constituents of bone.

The feces have been examined chemically by Berzelius, Simon, Marcet, Wehsarg, Ihrung,<sup>1</sup> and others. The human feces, on an average,

<sup>1</sup> Milne Edwards : Physiologie, tome vii. p 143.

may be said to consist of seventy-five parts of water to twenty-five of solid residue. In the latter there have been found among other substances the ammonium-magnesium phosphate, the magnesium phosphate, the calcium phosphate, and a small quantity of iron, fatty acids, occasionally cystin, *exeretin*<sup>1</sup> and *excretolic acid*, and *stercorin*;<sup>2</sup> this latter substance, as has already been mentioned, is according to Flint modified cholesterin. In the large intestine there is found carburetted hydrogen gas as well as nitrogen, hydrogen, and carbonic acid, which are also present in the small intestine and stomach. Oxygen gas is, however, found only in the stomach.

### DEFECATION.

In health the feces are usually discharged once in twenty-four hours. This rule, however, is far from being invariable, being modified by individual peculiarities.

Indeed, there are well authenticated cases of the act of defecation not having been performed during a period of eight years, and even longer, the unabsorbed food apparently having been either rejected by the mouth, or eliminated by the skin or kidneys. On the other hand, there seems to be no reason to doubt that there have been also cases in which the bowels were evacuated as often as twelve times daily, and that for thirty years, and yet without the health being affected.<sup>3</sup>

The feces are gradually passed through the contraction of the muscular fibres of the large intestine into the sigmoid flexure of the colon, where they accumulate, and are retained for some time. It is probably the descent of the feces from the sigmoid flexure of the colon, which is the immediate cause of the desire to defecate, the action being, to a certain extent as we shall see, under the control of the will. It is often thought that the feces accumulate in the rectum; the lower part of the rectum, however, in health is almost always empty. In old persons, or in those of a constipated habit the feces are often found there.

In the act of defecation, the feces first pass from the sigmoid flexure of the colon into the upper constricted part of the rectum, then into the lower portion, the sphincter muscle at first resisting, then giving away, through the inhibition (due to the stimulus of the feces) of the nervous centres controlling the sphincter ani, and the fecal mass leaves the body. The action is assisted by the levator ani, which favors the relaxation of the external sphincter, and by the compression of the viscera through the action of the diaphragm and the abdominal muscles. When the glottis is closed a point of support is further given to the latter muscles.

### RÉSUMÉ OF DIGESTION.

In concluding the subject of digestion, it does not appear to be superfluous to give a brief résumé of the different processes of which we have given a somewhat detailed account.

<sup>1</sup> Marcet: *Phil. Trans.*, 1854.

<sup>2</sup> Flint: *Physiology*, vol. ii. p. 399; vol. iii. p. 291.

<sup>3</sup> Dunglison: *Human Physiology*, 8th ed. vol. i. p. 191 Philadelphia, 1856. Chapman: *Lectures on the Diseases of Thoracic and Abdominal Viscera*, p. 294. Philadelphia, 1844.



The food, after having been taken into the mouth, is masticated, and through the action of the tongue and cheeks having been collected into a bolus, is then swallowed. The saliva poured into the mouth acts mechanically, aiding mastication and deglutition; and chemically, in converting some of the starch into glucose.

The albuminous substances of the food are converted into albuminose or peptones by the gastric juice, which has also the effect of dissolving, to some extent, the walls of the fat vesicles, the fat itself thus set free, however, being unaffected by this secretion. That part of the starch which has escaped conversion into glucose by the saliva either in the mouth or stomach, passes together with the cane sugar unchanged into the small intestine.

While the effect of the intestinal juice is limited to supplementing the action of the saliva upon starch, and that of the gastric juice upon albuminoids, the pancreatic juice not only acts upon both these kinds of food, converting the starch into glucose, and the albumen into albuminose, leucin, tyrosin, etc., but also converts cane sugar into glucose, and emulsifies and saponifies the fats. The bile assists in the emulsifying of fats, and promotes their absorption, it further retards putrefaction, and in stimulating the peristaltic action of the intestine acts as a natural purgative.

The conversion of starch into glucose, of albumen into albuminose, etc., appears to consist in a hydration of these substances, brought about by the presence of ptyalin, pepsin, etc., entering into the composition of the saliva, gastric juice, etc., respectively. These organic principles, to which the action of the alimentary secretions to a large extent is due, are elaborated out of the blood, and stored up during the intervals of digestion by the cells of which the glands consist. The ptyalin, pepsin, trypsin, pancreatin, etc., poured out at the moment of secretion, differ somewhat from the principles actually present in the gland during the intervals of digestion, being developed out of the latter at the moment of secretion. That the phenomenon of secretion is not one of mere filtration, is shown by the pressure exerted by the secretion, and that chemical action is going on is made evident through the heat and carbonic acid developed.

The contents of the large intestine consist essentially of the undigested part of the food (amounting to about one-fifth), decomposed bile, and of such digested principles as have not been absorbed. As these pass through the large intestine they gradually assume the consistence, color, odor, etc., of the feces. The latter accumulating in the sigmoid flexure of the colon, pass into the rectum and thence out of the body, their expulsion constituting the act of defecation.

## CHAPTER XI.

### ABSORPTION.

WHILE the digested food in the alimentary canal may be said to be inside of the body, using the word in its ordinary acceptation, physiologically it is still outside of it, for if the food simply remained in the alimentary canal it would be of no use for nutritive purposes. Indeed, unless the digested food gets into the blood, and is so carried to all parts of the organism, and repairs the waste of its tissues, and supplies the material for force, it might as well not be taken into the system at all. The process by which the digested food passes from the interior of the alimentary canal into the blood, either directly or indirectly, is known as absorption.

It is not to be understood, however, that absorption is by any means limited to the alimentary canal, or that the substances of which food consists are the only ones that can be absorbed. We shall soon see that oxygen is absorbed by the blood as it circulates through the lungs, that the skin will take up various substances, and that effusions found under certain circumstances in the cavities of the pleura, pericardium, peritoneum, etc., can be absorbed by these serous surfaces. Inasmuch, however, as we have just seen how the food is digested, naturally our study of absorption will begin with the consideration of the process as it goes on in the alimentary canal.

That the ancients were well aware that the human body absorbs, is evident from their writings. Thus Hippocrates,<sup>1</sup> for example, speaks of "the veins of the stomach and intestine attracting the clearest and most fluid parts of the solid and liquid food." Nothing, however, appears to have been known at that period of the lymphatic system. It is true, that in the writings of Galen there are preserved vague illusions, like those of Erasistratus,<sup>2</sup> "to arteries in the mesentery," "full of milk," and of Hierophilus<sup>3</sup> to "particular veins ending in certain glands," but the context shows that these old anatomists regarded the vessels alluded to, which were, no doubt, lymphatics, as nutrient, and not as absorbent in their function. Indeed, at that period the use of the arteries even was unknown, they being considered as air-keepers, as their etymology implies, rather than carriers of blood.

As the venous blood from the capillaries of the stomach and intestine is conveyed from the gastric and mesenteric veins by the portal vein to the liver, and thence by means of the hepatic vein and inferior vena cava to the heart (Fig. 84), a route evidently exists by which the digested food in the alimentary canal can get into the general circula-

<sup>1</sup> Opera Omnia, p. 119. Ludg. Batav., 1665.

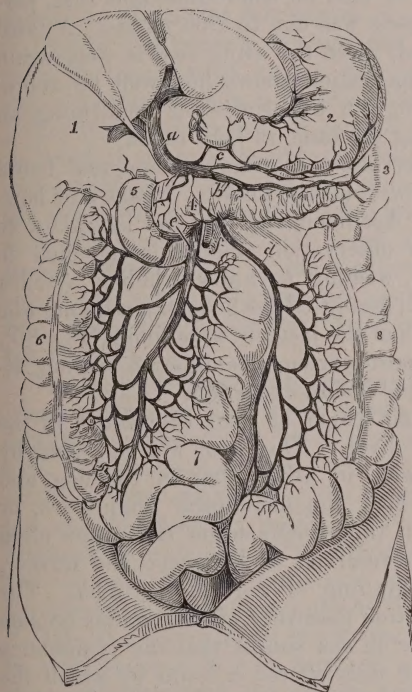
<sup>2</sup> Galenus Opera Omnia, tomus i. Cap. 5, p. 61. Venetiis, 1556.

<sup>3</sup> Ibid., Cap. 19, p. 141.



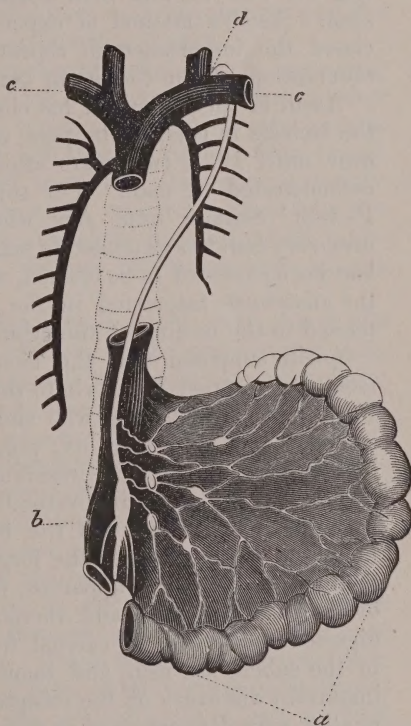
tion. The ancients were right, therefore, in considering the veins as a means of absorption, although at the same time they knew almost nothing of the course of the circulation. The first part of the lymphatic system discovered was the thoracic duct in the horse, described by Eustachius,<sup>1</sup> the Rôman anatomist, in 1563. Eustachius, while showing that the duct terminated in the subclavian vein, failed, however, to show where it commenced, and, therefore, did not learn its functional importance. Indeed, the discovery itself was forgotten, and

FIG. 84.



View of the principal branches of the vena portæ.  $\frac{1}{6}$ . 1. Lower surface of the right lobe of the liver. 2. Stomach. 3. Spleen 4. Pancreas. 5. Duodenum. 6. Ascending colon. 7. Small intestine. 8. Descending colon. a. Vena portæ dividing in the transverse fissure of the liver. b. Splenic vein. c. Right gastro-epiploic. d. Inferior mesenteric. e. Superior mesenteric vein. f. Superior mesenteric artery. (QUAIN.)

FIG. 85.



Lacteals, thoracic duct, etc. a. Intestine. b. Vena cava inferior. c, c. Right and left subclavian veins. d. Point of opening of thoracic duct into left subclavian. (DALTON.)

its significance was not appreciated till the following century. The history of the lymphatic system really begins with Gasparis Aselli's discovery, in 1622, in the dissecting amphitheatre at Pavia, of the lacteals of the small intestine in the dog. Aselli tells us in his work<sup>2</sup> on the lacteals that, on opening a dog to show some friends the recurrent laryngeal nerves, he was surprised to find in the mesentery in addition to

<sup>1</sup> Opusc. Anat., Antig 13, p. 280. Ludg. Batav., 1707.

<sup>2</sup> De Lactibus Sine Lacteis Venis, Cap. ix. Mediolani, MDCXXVII.

the arteries and veins, delicate, white lines, which, at first, he thought were nerves. On pricking one of them, however, and seeing a whitish, milk-like fluid escape, he exclaimed, like Archimedes of old, "Eureka!" for he felt he had made a great discovery. Wishing to confirm his discovery, Aselli, on the following day, opened a second dog, but was disappointed in not finding the white vessels seen on the previous occasion, and began to feel that he had been too hasty in announcing the discovery of a new set of vessels. On reflection, however, it occurred to Aselli that the first dog had been well fed before being opened, whereas, the second one had been deprived of food for some time, and that, perhaps, the absence of the white vessels was due to this cause. A third dog was well fed, and then opened, when the white vessels were again seen. Aselli's method of experimentation shows how well he appreciated the importance in repeating an experiment or confirming an observation, of the conditions being the same in both cases.

Aselli further extended his observations to other animals, and found the lacteals in cats, lambs, pigs, cows, and the horse. It was not, however, until 1628, two years after Aselli's death, that the lacteals were demonstrated in man. For this observation science is indebted to Peiresc,<sup>1</sup> Senator from Aix, who, wishing to know whether Aselli's discovery could be extended to man, permitted the body of a criminal who had been executed to be opened, when the lacteals were found (Fig. 85), the anatomists interested in the post-mortem examination having attended to the feeding of the criminal before execution.

Aselli supposed that the lacteals which he had discovered in the mesentery carried the chyle to the liver. This error was corrected by Pecquet,<sup>2</sup> a Frenchman, who showed, in 1649, that in the dog, and afterward in the horse, ox, pig, etc., the mesenteric lymphatics, or lacteals, terminated in a reservoir, the receptaculum chyli, now often called in honor of its discoverer the reservoir of Pecquet; and further, that this receptaculum was the beginning of the thoracic duct. The functional significance of the forgotten discovery of Eustachius became then for the first time apparent, for it was shown that the lymphatics of the small intestine and thoracic duct offered a route by which the digested food could be carried from the alimentary canal to the blood in the subclavian vein, and thence to the heart. Two years after the important discovery of the receptaculum chyli—that is, in 1651—lymphatics were demonstrated in the liver and other parts of the body by Rudbeck,<sup>3</sup> and their course and connection with each other and the mesenteric lymphatics made out. These vessels were, however, called by the Swedish anatomist aquiferous, or serous vessels.

A few months after Rudbeck's discovery, they were again described by Bartholinus,<sup>4</sup> Professor of Anatomy at Copenhagen, who designated them lymphatics, the name they now bear. Bartholinus appears also the first, so far as the author has been able to learn, to have seen the

<sup>1</sup> Milne Edwards: *Physiologie*, tome v. p. 450. Paris, 1859. Berard: *Physiologie*, tome ii. p. 565. Paris, 1849.

<sup>2</sup> Joannis Pecqueti: *Diæpæi Experimenta Nova Anatomica*, Cap v. and vi. Amst., 1661.

<sup>3</sup> Olai Rudbeck: *Nova Exercitatio Anatomica exhibens ductos hepaticos aquosos vasa glandularum serosa*. Clericus & Mangetus, Bibliotheca Anatomica, tomus ii. p. 629. Genevæ, 1699.

<sup>4</sup> Thomæ Bartholinæ: *Anatomia de Lacteis Thoracis et vases Lymphaticis*. Hagæ Com, 1666.



reservoir of Pecquet in man, which he figures,<sup>1</sup> the thoracic duct having been discovered by Van Horne, in 1652.<sup>2</sup> Jolyffe,<sup>3</sup> a student of medicine at Cambridge, England, seems also to have discovered the lymphatics independently of both Rudbeck and Bartholinus. While Jolyffe, however, did not publish anything in reference to the lymphatics, he nevertheless made preparations of them, which Glisson<sup>4</sup> states to have seen in 1652.

In the following century the lymphatic system was studied in man and animals by many anatomists, especially by William<sup>5</sup> and John Hunter,<sup>6</sup> Hewson,<sup>7</sup> Monro,<sup>8</sup> Cruikshank,<sup>9</sup> the great work of Mascagni<sup>10</sup> appearing also about this period.

During the present century the lymphatic system has been most carefully investigated by the best anatomists and physiologists of the day. Let us consider now briefly its structure and uses.

The lymphatic system in general consists of vessels which, beginning in the skin, mucous membrane, glands, etc., converge toward each other and gradually uniting with larger and larger trunks finally terminate in the subclavian veins as the right and left thoracic ducts. The lymph from the right side of the head and that from the upper extremity passes into the blood of the right subclavian vein, while that from the rest of the body, including the lymph and chyle from the small intestine, is conveyed into the blood of the left subclavian vein by the left thoracic duct. right side  
thorax

The lymphatics, in their general structure, resemble very closely the veins, consisting, like these vessels, of three coats, an external one, composed essentially of white fibrous tissue; a middle muscular elastic coat, the elastic muscular fibres being arranged circularly, and an internal epithelial layer constituting the internal coat. The lymphatics also contain valves, consisting usually of two semilunar folds. The lymphatics originate as plexuses, or as continuations of the interlacunar spaces of the tissues. These spaces are usually lined with a continuation of the internal epithelial coat of the lymphatics.

Here and there, along the course of the lymphatics, solid bodies may be seen varying in size between a hemp seed and an almond, which apparently surround the vessels, and through which the contents must pass in their way to the thoracic ducts. These bodies are the lymphatic glands, and are more evident in certain parts of the body than in others, being well developed, for example, in the cervical, axillary, and inguinal regions. The minute structure and uses of these glands will be described when the elaboration of the blood is considered. The lymphatics not only connect the interstices of the tissues with the blood, beginning in the one and ending in the other, but they also communicate with the

<sup>1</sup> Compare Sprengel, *Hist. de la médecine*, tome quatrieme, p. 212.

<sup>2</sup> Hyrtl: *Lehrbuch der Anatomie*, 1870, S. 43.

<sup>3</sup> Sprengel, *op. cit.*, p. 210.

<sup>4</sup> Franciscus Glissonii: *Anatomia Hepatis*, p. 308. Clericus & Mangetus, *Bibliotheca Anat.*, tome ii. Gen. 1699.

<sup>5</sup> *Medical Commentaries*, William Hunter. London, 1777.

<sup>6</sup> Works of John Hunter, Palmer's edition, vol. 1.

<sup>7</sup> Phil. Trans., 1767 and 1768, and *Lymphatic System in the Human Subject and in other Animals*, by William Hewson. London, 1774.

<sup>8</sup> Alex. Monro: *Anatomy*, p. 310. Edinburgh, 1782.

<sup>9</sup> *The Anatomy of the Absorbing Vessels of the Human Body*. By William Cruikshank. Lond. 1786.

<sup>10</sup> *Vasorum Lymphaticorum Corporis Humani*. Paulo Mascagni, Senis, 1787.

serous cavities. Indeed, the serous cavities, like the peritoneum, pleura, etc., can be regarded morphologically, as dilated lymphatic sacs lying<sup>1</sup> between the viscera, these inter-organic spaces representing on a large scale the minute inter-lacunar spaces, which we have just seen often constitute the beginning of a lymphatic.

Lymphatics are found very generally throughout the system. According to Sappey,<sup>2</sup> however, they have never been demonstrated in teeth, hair, nails, etc. Possibly, though, future researches may show that lymphatics exist even in such situations.

It is only within recent years that the fluid contained in the lymphatics, or lymph, has been satisfactorily studied. The lymph obtained by experiments made upon animals in the beginning of this century by Muller,<sup>3</sup> Magendie,<sup>4</sup> Collard de Martigny,<sup>5</sup> etc., was in too small quantities to admit of thorough analysis, while the observations of Marchand, Colberg,<sup>6</sup> and Nasse,<sup>7</sup> were unsatisfactory, as the human lymph collected in these cases was probably abnormal. While it had been tried before, it was only in 1853 that Colin<sup>8</sup> succeeded in making a fistula in the thoracic duct of the horse, and showed by this method of investigation that large quantities of normal lymph could be obtained in a short space of time. Colin afterward extended his observations, experimenting in the same way on other animals, and his method is the one now employed by physiologists in the investigation of the lymph.

Lymph is a transparent, yellowish, alkaline liquid; the opaline appearance that it sometimes exhibits is due to small particles of fat, while the rosy tint that is often observed in it is caused by the red corpuscles that have passed into it from the blood. When examined under the microscope, lymph is seen to consist of a liquor, and small bodies floating in it, the lymph corpuscles or globules. These measure on an average about  $\frac{1}{2500}$ th of an inch; they are homogeneous or granular in appearance, and are undistinguishable, as we shall see from the white-corpuscles of the blood. When we come to study the red blood-corpuscles in man and animals, one of the most striking facts to be noted will be the great difference in their size. As regards the lymph or white corpuscles, however, it has been shown by Gulliver<sup>9</sup> and others that their average diameter bears no relation to that of the red corpuscle, being as large, for example, in the musk deer, where the red corpuscle is small, as in man where it is large. Further, the white corpuscle in birds is usually smaller than that of mammals, whereas the red corpuscle of birds is larger than that of the mammal, while in the frog both the white corpuscle and the red are larger than those of the mammal.

Like the blood, the lymph coagulates when drawn from the living body. This is due in both cases to the fibrin which these fluids contain. The lymph clot, however, is less solid than that of the blood, and little or no serum exudes from it. The clot consists not only of fibrin, but of the lymph corpuscles that the lymph carries.

<sup>1</sup> The Lymphatic System, p. 222. Recklinghausen: Stricker's Histology. New York, 1872.

<sup>2</sup> Anatomie, tome deuxième, p. 791.

<sup>3</sup> Annales des Sciences, 1834, tome i. p. 340. <sup>4</sup> Precis de Physiologie, tome ii. p. 192. Paris, 1836.

<sup>5</sup> Journ. de Phys. de Magendie, 1828, tome viii. p. 152.

<sup>6</sup> Muller's Archiv, 1838, p. 139.

<sup>7</sup> Zeits. für Phys. von Treviranus, 1832.

<sup>8</sup> Phys. Camp., 1856, tome ii. p. 100,

<sup>9</sup> The Works of William Hewson, p. 244. London, 1846.



Chemically, the liquor of the lymph differs, as we shall see, from the liquor of the blood quantitatively, rather than qualitatively, both these fluids consisting essentially of water, albumen, fibrin, and salts. Usually the lymph (Table XXXIX.) contains as much fibrin as the blood, but less albumen. There is more water in the lymph than in the blood, but the amount of salts in both liquids is about the same. From the fact of these two liquids, the liquors of the lymph and blood, being alike in their chemical composition,<sup>1</sup> one may naturally infer that the lymph is nothing but that part of the blood which has escaped, leaked out, so to speak, from the vascular system into the surrounding tissues, and afterward is soaked up by the lymphatics.

TABLE XXXIX.—COMPOSITION OF LYMPH AND CHYLE.

|                         | Lymph. <sup>2</sup> | Chyle. <sup>3</sup> |
|-------------------------|---------------------|---------------------|
| Water . . . . .         | 939.87              | 904.8               |
| Solid residue . . . . . | 60.13               | 95.2                |
| Fibrin . . . . .        | 0.56                |                     |
| Albumen . . . . .       | 42.75               | 70.8                |
| Fat . . . . .           | 3.82                | 9.2                 |
| Extractives . . . . .   | 5.70                | 10.8                |
| Salts . . . . .         | 7.30                | 4.4                 |

It has already been mentioned that the red corpuscles often found in the lymph are really red blood-corpuscles that have escaped from the capillaries. While it is possible that some of the lymph corpuscles may also be only white blood-corpuscles that have passed from the blood with the red ones into the lymph, the lymph corpuscles in general appear to originate in an entirely different manner, there being good reasons for supposing that they are produced in the lymphatic glands, spleen, etc. The consideration of the origin of the lymph, or white corpuscles, and their relation to the red ones and the glands just mentioned, we will, however, defer until the blood is studied, and pass on to the consideration of the quantity of the lymph, and the causes of its flow through the system.

Naturally, from the conditions of the case, the amount of lymph can be estimated only approximately. In making a fistula of the thoracic duct, the circulation must be interfered with to a certain extent, and this circumstance will be a source of error in deducting the amount of lymph in the body from that poured out through the fistula. Though the exact amount of lymph cannot be estimated, it is safe to say that the amount is probably underestimated, rather than exaggerated. Colin<sup>4</sup> obtained from the horse about a pound of lymph in an hour, and as much as four pounds, and even more, from the ox in the same period of time. Dalton<sup>5</sup> estimated that in twenty-four hours there are between three and a half to four pounds, or 2000 grammes, of lymph produced in a man of average weight. Various causes have been assigned by physiologists for the flow of the lymph. Of these some, no doubt, are

<sup>1</sup> The lymph, according to the investigations of Ludwig (Arbeiten, 1871, S. 121) and his pupils, contains, like the blood, also gases, carbonic acid and nitrogen being most commonly found.

<sup>2</sup> Gubler and Sulvenne : Gaz. Méd. de Paris, 1854, p. 454.

<sup>3</sup> Rees : Phil. Trans., 1842, p. 81.

<sup>4</sup> Physiologie Comparée, tome ii. p. 106.

<sup>5</sup> Physiology, 1882, p. 323.

more important than others. Let us consider them briefly. One of the principal causes of the flow of the lymph is undoubtedly the *vis a tergo* resulting from the constant passing of the serum of the blood into the lymphatic system, and as the lymph, on account of the valves (Fig. 86) in the vessels, must flow always from the periphery or the radicles of the system, toward the great trunks and bloodvessels, each successive addition of serum to the lymphatic system will act as a force propelling forward the lymph already there.

FIG. 86.



Valves of the lymphatics. (SAPPEY.)

From the fact that the lymphatics contain unstriped muscular fibre, it is probable that these vessels at times contract upon their contents. This action, however, would appear to be slight, inasmuch as the rhythmical contractions of the lymphatics in mammals are rarely observed. It should be mentioned in this connection, however, that frogs, toads, lizards, etc., the lymphatics of which are unprovided with valves, possess the so-called lymphatic hearts. The latter are dilated portions of the lymphatics, exhibiting contractility, and which pulsate regularly.

The influence of muscular contractions upon the flow of the lymph must not be forgotten, for pressure upon the lymphatics from this source will have the same effect as we shall see it has in accelerating the flow of blood in the veins.

From the disposition of the terminal portion of the lymphatic system in the thoracic cavity, it might naturally be inferred that during inspiration, inasmuch as all the parts are dilated, that the flow of lymph into the thoracic ducts would be increased, and that, during expiration, as all of the parts are contracted, the lymph will then flow onward into the left subclavian vein, regurgitation being impossible through the presence of valves. Experiment has shown that such is in fact the case. With each inspiration the thoracic ducts become dilated through the increased flow of lymph, at that moment the lymph flows freely from the right thoracic duct into the right subclavian vein. With each expiration the lymph is expelled with increased force from the left thoracic duct into the left subclavian vein, and when a fistula is made in that situation the lymph issues as an intermittent jet.

Of the different causes just given for the flow of the lymph, it would appear that the *vis a tergo* and the respiratory movements are the most important, the contractility of the vessels and the pressure of surrounding parts being of secondary importance.

Up to this moment, in speaking of the lymphatic system, we have only alluded incidentally to the lymphatics of the small intestine, or the lacteals. As these vessels have a special interest for us in connection with the absorption of the digested food, let us study them now a little more in detail.

The lacteals, or lymphatics of the small intestine, begin in the villi,



which structures we only alluded to in speaking of the alimentary canal, reserving for the present moment their more detailed consideration. The villi are small processes of the mucous membrane of the small intestine, measuring on an average about the one-thirty-sixth of an inch in length, and about the one-seventy-second of an inch in breadth. They are usually conical, and flattened in form, though sometimes cylindrical, or terminating in an enlarged or clubbed-like extremity. The villi are largest and most numerous in the duodenum and the so-called jejunum. They are closely set upon the inner surface of the intestine over the *valvulae conniventes*, as well as between the same, and give rise to the characteristic velvety appearance of the mucous membrane in this situation.

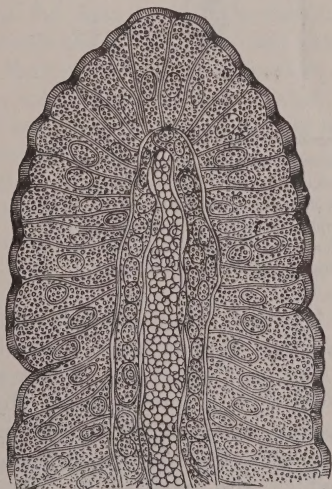
It has been estimated that in the upper part of the small intestine there are fifty to ninety villi to the square line, their total number amounting to about four millions. The villi can be well seen by examining a piece of intestine under water with a simple lens, the mucus having been first removed by gentle washing. When studied with the microscope the villus is seen to consist of a prolongation of the epithelial layer of the mucous membrane of the intestine, enclosing a network of bloodvessels, the beginning of the lymphatics, or the lacteals, and some plain muscular fibres. These structures are held together

FIG. 87.



Villus of man with lacteal and bloodvessels injected. (TEICHMANN.)

FIG. 88.



Villus of man showing lacteal surrounded by epithelial cells. (FREY.)

and supported by lymphoid or retiform tissue, which, at the surface, is condensed into a basement membrane, upon which the epithelial cells rest.

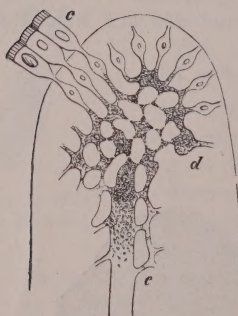
Up to this time it is doubtful if nerves have been demonstrated in

the villi. It is very probable, however, that they are present. Each villi usually receives one arterial twig, which, after penetrating it, breaks up into capillaries situated just beneath the basement membrane. The blood is returned usually by one vein. The lymphatic, or the lacteal, begins in the centre of the villus, usually as a single vessel (Fig. 87), with a closed and somewhat expanded extremity. Its calibre is considerably larger than that of the capillary bloodvessels surrounding it.

The lacteal within the villus, like the lymphatics elsewhere, is surrounded by a delicate layer of flattened epithelioid cells (Fig. 88). These are connected with the cells of the basement membrane through those of the lymphoid or connective tissue lying between (Fig. 89).

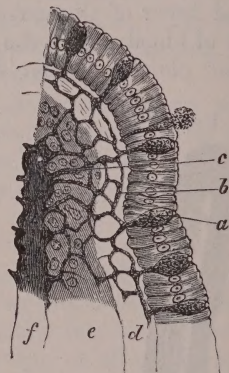
The columnar epithelial cells which cover the villi, and also the surface of the mucous membrane, and which are prolonged into the tubular glands, present a granular appearance with an oval nucleus. They terminate toward the basement membrane in a tapering manner, and measure about the  $\frac{1}{1000}$ th of an inch ( $\frac{1}{40}$ th of a mm.) in length.

FIG. 89.



Diagrammatic representation of the origin of the lacteals in a villus, according to Funke. *e.* Central lacteal. *d.* Connective-tissue corpuscles with the communicating branches. *c.* Columnar epithelial cells, the attached extremities of which are directly contiguous with the connective-tissue corpuscles. (CARPENTER.)

FIG. 90.



Origin of the lacteals, according to Letzerich. The cells marked *a*, are cup or goblet cells, and are seen to be intercalated amongst the columnar epithelial cells, and to communicate with a delicate plexus, *b*, that opens at various points into the central lacteal, *c, f.* *d.* Layer of clear connective tissue. *e.* Connective tissue with numerous nuclei. (CARPENTER.)

Their free end, or the surface looking toward the interior of the intestine, consists of a layer of a highly refractory substance, with vertical striæ running through it. These striæ have been regarded by Kolliker<sup>1</sup> and Funke<sup>2</sup> as minute canals; Henle,<sup>3</sup> however, considers them to be solid rods. Some of these columnar cells usually contain mucus, and swell up upon the addition of water into the so-called goblet cells (Fig. 90), which are regarded by Letzerich<sup>4</sup> as the true beginning of the absorbent system.

The lymphatic or lacteal, after emerging from the villus, passes into

<sup>1</sup> Gewebelehre, S. 409. Leipzig, 1867.

<sup>2</sup> Anatomie, Eingeweidelehre, S. 177. Braunschweig, 1873.

<sup>4</sup> Virchow's Archiv, Band xxxix. S. 435.

<sup>2</sup> Physiologie, S. 222. Leipzig, 1876.



the lymphatics of the intestine. These are usually described as consisting of two sets, the deep and superficial. The latter pass in the mesentery to the lymphatic glands. The lymphatics coming from the latter, as we have seen, converge toward the receptaculum chyli.

During the intervals of digestion the lymphatics of the small intestine, or the lacteals, contain lymph, undistinguishable from that of the lymphatics of the rest of the body. During digestion and absorption, however, and more especially when fatty articles have constituted part of the food, the epithelial cells of the villi, and the lymphatics of the small intestine, are then filled with the chyle. The chyle is a coagulable, alkaline, opaque, whitish, milky-like fluid, hence the name of the lacteals given to the lymphatics of the small intestine, in which it is found.

The chyle (Table XXXIX.), however, is only the lymph with the products of digestion added to it, and as the lacteals absorb principally the fat, the essential difference between the chyle and the lymph is that the former contains a great quantity of fat, the latter usually only a trace. In reference to any analysis of the chyle, it must not be forgotten that its composition will differ according to whether the portion examined has been taken from the lacteals or the thoracic duct. Indeed, chyle drawn from the thoracic duct is not pure chyle, but chyle mixed with the lymph which has been brought from the extremities to the receptaculum chyli, and thence passed into the thoracic duct.

The chyle of the thoracic duct will contain, therefore, less fat and other solid constituents, being diluted with the lymph mixed with it. Further, the amount of fat in the chyle will be variable, depending upon the diet of the man or animal examined. Thus, the chyle of a carnivorous animal will contain more fat than that of a herbivorous one, the food of the former being richer in fat than that of the latter. At one time it was supposed that the lacteals absorbed exclusively the fatty substances, but it is now known that they also take up, at least in small quantities, albuminoid and saccharine substances, salts and water.

Of the amount of the chyle poured into the thoracic duct, it is impossible to give even an approximate estimate.

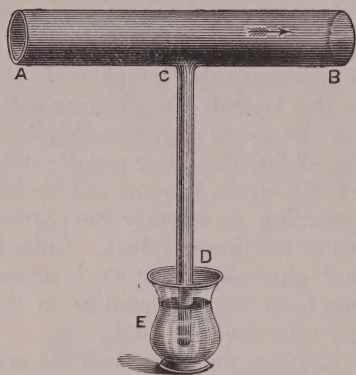
When examined microscopically, the milky appearance of the chyle is seen to be due to an immense number of very minute fatty granules, which constitute the so-called molecular base of the chyle, and which measure on an average from the  $\frac{1}{12000}$ th of an inch to the  $\frac{1}{2500}$ th of an inch in diameter. These granules appear to be coated with albumen, which probably prevents their running together and coalescing. The so-called chyle corpuscles found in greater or less number in the chyle, do not differ from those of the lymph or blood, and will be considered again when the latter fluid is studied.

What has been already stated in reference to the supposed causes of the flow of the lymph will apply equally well to that of the chyle; but there are certain conditions, in addition to those already mentioned, which appear to influence favorably the flow of the chyle, and so deserve a passing notice. It will be remembered that, in speaking of the structure of the villi, allusion was made to the plain muscular fibre that they contain. These muscular fibres are dispersed longitudinally around the lacteal, and their contraction will obviously retract the

villus. The effect of the action of these muscular fibres will then be to force the contents of the lacteal out of the villus into the superficial lymphatics. These muscular fibres have probably, then, some importance in aiding the flow of the chyle toward the thoracic duct.

It will be remembered that the thoracic duct, in passing to the left side to terminate in the subclavian vein, passes behind the aorta. Haller<sup>1</sup> called attention to this fact as an important one, the great

FIG. 91.



Principle of Venturi. (DRAPER.)

physiologist considering that the contractions of the aorta in compressing the duct would favor the flow of the chyle and lymph toward the subclavian vein. Recently, Prof. Draper<sup>2</sup> has further suggested that the flow of blood in the subclavian vein exerts a suction force upon the contents of the thoracic duct, basing his view upon the hydraulic principle of Venturi, that, if into a tube (Fig. 91) through which a current of water is steadily flowing another tube opens, its more distant end being in communication with a reservoir of water, a current will be likewise established, and the reservoir be emptied of its contents. The

anatomical disposition of the parts, together with the fact that the flow of the chyle ceases with the flow of the blood, appear to show the close dependence of the movement of the one on that of the other. It will be remembered that, up to the time that the lymphatics were discovered, absorption was considered to be effected by the veins only. After the discovery of the lymphatics, however, physiologists fell into the opposite error of attributing absorption solely to the lymphatics, denying that the veins took any share in this process. Indeed, it was not until the present century that it was experimentally demonstrated that the veins as well as the lymphatics absorb. Apart, however, from any experimental evidence, the facts of comparative anatomy alone might have shown that of the two sets of vessels, so far as the absorption of the digested food is concerned, the veins play a more important part than the lymphatics. Thus it is well known<sup>3</sup> that in the amphioxus, the lowest of the vertebrata, and in all the invertebrata, the lymphatic system is absent. In these animals, therefore, absorption is carried on solely by veins. Further, while the lymphatic system is present in fishes, batrachia, reptiles, and birds, it is only in the mammalia that it acquires the functional importance that we have ascribed to it.

Indeed, according to Bernard,<sup>4</sup> the name lacteal cannot be properly applied to the lymphatics of the small intestine in the oviparous verte-

<sup>1</sup> *Elementa Physiologiae*, tomus vii. p. 237.

<sup>2</sup> *Physiology*, 1878, p. 79.

<sup>3</sup> Owen: *Comp. Anat. of Vertebrates*, vol. i. p. 455; vol. ii. p. 180; vol. iii. p. 504. Milne Edwards: *Physiologie*, tome iv. p. 462. Gegenbaur *Vergleichende Anatomie*, S. 857. Leipzig, 1870.

<sup>4</sup> *Physiologie Experimentale*, tome ii. p. 312.



brates, since these lymphatics contain always, even during digestion, with few exceptions, a clear, transparent lymph instead of chyle, an opaque, whitish fluid, the fat in these animals being taken up, not by the so-called lacteals, but by the portal vein, the greater part of it being thence carried to the renal veins (Jacobsen's system), and so to the vena cava.

Inasmuch as absorption is carried on by the veins in the lower animals, we would naturally infer that these vessels must be of great importance in this respect in man and the mammalia. That such is the case can be readily demonstrated experimentally. Magendie<sup>1</sup> appears to have been the first to show conclusively by experiment that absorption takes place by the bloodvessels.

Of his many remarkable and accurate experiments, the following may be mentioned: In one experiment, the abdomen of a dog that had been well fed some hours previously was opened, and a loop of the intestine drawn out. Ligatures were placed around this loop at a distance of about fifteen inches apart. The lymphatics arising from this portion of the intestine being all ligated in two places, were divided between the ligatures. Of the five mesenteric arteries and veins passing into the general vascular system, four were divided and ligated so that the loop of the intestine remained in connection with the rest of the system by only a single vein and artery, even the cellular coat of which was dissected off, so as to remove all doubt of there being a trace of a lymphatic left. Some upas was then introduced into the loop of the intestine prepared in the above manner, which was then replaced in the abdomen, and in a few minutes the characteristic symptoms of poisoning appeared, showing that the upas had been absorbed by the vein.

In another experiment, where the poison was introduced into the foot, the only connection between the limb and the rest of the body was through two quills, introduced into the divided femoral bloodvessels, the rest of the parts having been dissected off. In this case, also, the only possible means by which the poison could pass into the general system and make its effects evident was through the circulating blood.

The experiments of Magendie were immediately fully confirmed by Tiedemann and Gmelin,<sup>2</sup> who showed, in an elaborate series of experiments, that different kinds of foods, odorous and coloring matters, saline and metallic substances were absorbed by the radicles of the portal vein as well as by the lymphatics of the small intestine.

Segalas<sup>3</sup> modified the experiments of Magendie, and further confirmed them by demonstrating that a poison like nux vomica, when introduced into the alimentary canal, fails to produce its characteristic effects so long as the circulation of the blood is interrupted, or when the blood carrying the poison from the intestine is allowed to escape from the vein and not pass into the general circulation.

Magendie's experiments were also fully repeated and confirmed in this city by Drs. Harlan, Lawrence, and Coates, the committee ap-

<sup>1</sup> Journal de Physiologie, p. 18. Paris, 1821.

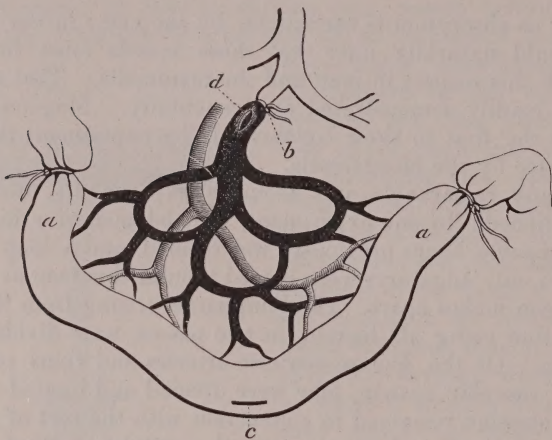
<sup>2</sup> Recherches sur la route qui prennent diverses substances pour passer d'Estomac et du Canal intestinal dans le Sang. Paris, 1821.

<sup>3</sup> Journal de Physiologie, tome ii. p. 117. Paris, 1822.

pointed by the Academy of Medicine of Philadelphia to investigate the subject.<sup>1</sup>

A convenient method of demonstrating venous absorption is to open the abdomen of a frog, withdraw a loop of the intestine, and ligate it

FIG. 92.



*aa.* Intestine. *b.* Point of ligation of mesenteric vein. *c.* Opening in intestine for introduction of poison. *d.* Opening in mesenteric vein behind the ligation. (DALTON.)

in two places, cut away all the mesentery, leaving only a single artery and vein, and introduce a solution of ferrocyanide of potassium into the intestine by an opening made in the latter, replace the loop within the abdomen, and, after a few minutes, open one of the veins of the foot. On testing the blood for the ferrocyanide of potassium by adding tincture of the chloride of iron, the presence of the salt introduced into the intestine will become at once evident, through the formation of Prussian blue, the latter being best demonstrated by adding the perchloride of iron to the serum, the blood having been allowed to stand, or to a clear extract of the blood made by boiling the latter with a little sodium sulphate and filtering.

It is obvious that the only means by which the salt of potassium could pass from the intestine into the general circulation, and thence into the blood of the extremities, was by means of the vein left in the mesentery. The above experiment is essentially the same as that performed by Panizza<sup>2</sup> upon the horse.

We have seen that while the principal function of the lymphatics of the small intestine is to absorb fat, nevertheless they can and do take up albuminose, glucose, and water; on the other hand, the mesenteric veins, in addition to absorbing these latter substances, take up also, at times, considerable quantities of fat. Briefly, then, the functions of the lymphatic and venous absorbents are essentially the same; as a rule, however, the fats pass into the blood by the one route, the remaining alimentary substances by the other.

<sup>1</sup> Phila. Journal of the Med. and Phys. Sciences, 1821, vol. iii. p. 273, and 1822, vol. v. p. 327.

<sup>2</sup> De l'absorption veineuse. Paris, 1843.



As digestion is only completed in the small intestine, we considered it most appropriate to begin the study of absorption there. It must not be supposed, however, that nothing is absorbed by the stomach. On the contrary, there can be little doubt that water and other liquids are very rapidly taken into the blood there, and also albuminose and whatever glucose may be present. Experiments made upon animals where the pylorus has been tied, and water introduced into the stomach, showed that in a very short time the liquid is absorbed by that viscus.

The difference of opinion prevailing among experimenters in reference to the absorbing power of the stomach is due, no doubt, to the fact that this differs very considerably in animals. Thus, water is absorbed very slowly by the stomach in the horse, and in small quantities; though very rapidly, and in considerable quantity, in the dog and rabbit.<sup>1</sup> So far as man is concerned, the case of Busch,<sup>2</sup> already referred to, showed conclusively the absorbing powers of the human stomach, almost all the sugar eaten being absorbed in this part of the alimentary canal, as well as a considerable quantity of the albumen.

It is well known to physicians that human beings can be kept alive for months by enemata, the rectum absorbing very rapidly; its capacity for taking up water, for example, is probably as great as that of the stomach. We have seen, also, that the rest of the large intestine absorbs to a large extent.

As the digested food ordinarily, however, is absorbed before it reaches this part of the alimentary canal, further reference to absorption in this respect is not necessary.

That the mucous membrane of the mouth is capable, also, of absorbing is shown from the effects observed when tobacco-juice is retained, even for a short time, in the mouth. Food, however, remains for such a short time in the mouth, that little chance is offered for its absorption in this part of the alimentary canal.

Absorption by the skin and by serous cavities, and the influence of the nervous system and the circulation upon this function, can be more conveniently treated when these subjects are especially considered. We will pass on, therefore, to the study of the causes of absorption.

<sup>1</sup> Colin, *op. cit.*, tome ii. p. 29.

<sup>2</sup> *Op. cit.*, p. 140.

## CHAPTER XII.

### OSMOSIS.

WE have seen that during absorption the digested food passes from the interior of the alimentary canal into the veins and lymphatics. The investigation of the causes of the phenomena of absorption resolves itself, therefore, into the determination of the conditions on which depend the passage of the liquid or semi-liquid albuminose, glucose, etc., and emulsified fat through the epithelium of the alimentary canal and the wall of the capillary or lymphatic into the blood or lymph.

In physical science the diffusion of liquids into each other when separated by a membrane is known as osmosis. Let us consider, briefly, what is understood by the term osmosis, and see whether the facts of absorption that we have described can be explained by this principle.

The name of Dutrochet is invariably associated with any discussion of the phenomena of osmosis. The history of the subject teaches us, however, that the discovery of this important physical principle, like that of all others, was not a sudden, but a gradual one. Many of the phenomena had been observed, and numerous experiments bearing upon the subject had been performed and recorded before the time of the distinguished French physiologist. The merit of Dutrochet consisted in not only devising and performing new experiments, but of generalizing the facts of osmosis, and applying them to the explanation of absorption in living beings.

The first recorded experiment, so far as I have been able to learn, bearing upon the subject of osmosis, was performed as long ago as 1748 by the Abbe Nollet,<sup>1</sup> who, in investigating the causes of the boiling of liquids, showed that when a vial of alcohol covered with a bladder was immersed in water the bladder became convex, the water diffusing through the membrane into the alcohol, whereas, if the vial was filled with water, and immersed in alcohol, the bladder became concave, the water diffusing through the membrane from the vial into the alcohol.

Nollet further showed that, while water passed readily through the bladder, alcohol only did so with difficulty and under pressure. In 1802 Parrot<sup>2</sup> observed that an egg, from which the shell had been removed, would absorb water, the liquid traversing the egg membrane. The fact, however, was only noted, no further application being made of it. Equally unfruitful were the observations of Sœmmering<sup>3</sup> and Van Mons,<sup>4</sup> who, about 1812, called attention to the fact that spirituous liquors became more condensed through the evaporation of their water,

<sup>1</sup> *Memoires de l'Academie des Sciences*, p. 101. Paris, 1748.

<sup>2</sup> *Bulletin scient. de l'Acad. de Petersburg*, 1840, t. vii. p. 346.

<sup>3</sup> *Gilbert's Annalen der Physik*, 1819, t. lxi. p. 104.

<sup>4</sup> *Annales gén. des sciences phys.*, t. i. p. 76. Bruxelles, 1819.



the vessels containing them<sup>are</sup> are closed by membranous stoppers, the water passing through the membranes. *was*

Porrett,<sup>1</sup> in 1816, noted that a galvanic current influenced the passage of water through a membranous septum, the fluid accumulating around the negative pole.

The observations just mentioned have for us now but little more than an historical interest, but the experiments of Lebkuchner,<sup>2</sup> in 1813, and Magendie,<sup>3</sup> in 1820, are very important still, as being the first in which it was positively demonstrated that various solutions would pass readily through membranes into the blood of the living animal. Lebkuchner showed that potassium ferrocyanide placed upon the jugular vein of a living rabbit in a few minutes passed into the blood, and could be detected in the blood of the jugular vein of the opposite side when tested for by adding sulphate of iron. Magendie dissected out the jugular vein of a dog, and placing it upon a card, poured upon it a solution of nuxvomica, taking the precaution of not letting the poison touch anything but the card and vein, and observed in a few minutes the symptoms of poisoning.

Important observations and experiments bearing upon the subject of osmosis, were further made in 1822, by Fischer,<sup>4</sup> of Breslau. This experimenter not only constructed what is now called an endosmometer, but showed that when the tube of the apparatus closed by animal membrane, and filled with a saline solution, was plunged into pure water, the water passed through the membrane into the saline solution, while the latter passed in the reverse direction through the membrane into the water. Fischer also noted some of the conditions influencing these currents, observing that they continued until the liquids were of the same density, and that they were active according to the thinness of the membrane used. Notwithstanding the value of the observations and experiment referred to in the above historical résumé, they do not appear to have received from physiologists the attention they merited, and would not have assumed their present importance had it not been for the later investigations of Dutrochet.<sup>5</sup>

This able investigator described thoroughly the passage of liquids through animal membranes: he showed the influence of different liquids used, measured the force of the currents, constructed the endosmometer, and called particular attention to the currents, naming them endosmotic and exosmotic, according as they passed into the tube from the surrounding liquid, or in the reverse direction, and applied the facts to the explanation of physiological phenomena. Since then the subject of osmosis has been most thoroughly investigated by Graham.<sup>6</sup> This physicist discards the terms endosmosis and exosmosis, considering that there is but one current, the inward one, and designating it by the term osmotic, and the whole phenomena as osmosis.

According to Graham, the molecules of the salt in the outward current travel by diffusion through the porous membrane. "It is not the

<sup>1</sup> Annals of Philosophy, 1816, vol. viii. p. 74.

<sup>2</sup> Archiv Général de Médecine, t. vii. p. 439. Paris, 1825.

<sup>3</sup> Journal de Phys., tome i. p. 1. Paris, 1821.

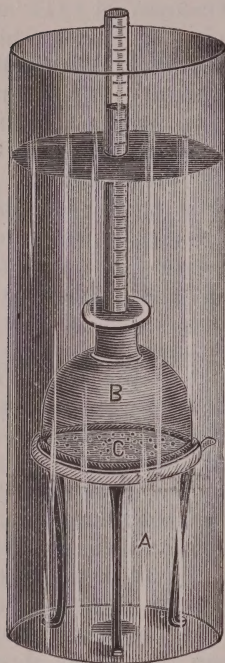
<sup>4</sup> Gilbert's Annalen der Physik, 1822, Band lxxii. S. 301.

<sup>5</sup> Memoires pour servir a la Histoire Anatomiques et Physiologiques des Animaux, tome i. Paris, 1837.

<sup>6</sup> Osmotic Force, Phil. Trans., 1854, p. 178.

whole saline liquid which moves outward, but merely the molecules of salt, their water of solution being passed, the inward current of water, on the other hand, appearing to be a true, sensible stream." According to this view, the only true current in the endosmometer (Fig. 93) is that

FIG. 93.



Graham's endosmometer. (FLINT.)

of the water from the jar (A) through the membrane (C) into the bulbous tube (B) containing the yellow saline, consisting of a solution of potassium bichromate, the apparent outward movement from the jar (B) into the water in A, being due to the diffusion of the molecules of the salt. So far, however, as the physiologist is concerned, the important fact in this experiment is, that there is an exchange going on, the water passing one way, the salt the other. A more delicate and interesting way of illustrating osmosis is to replace the jar of the last experiment with an egg prepared in the following way: At one end of the egg the shell is removed in such a way as to leave the lining membrane of the egg intact; at the other end, shell and membrane are both perforated sufficiently to permit the passing of a glass tube into the egg; the tube is held securely to the egg by sealing wax. The egg is then placed in a wine-glass of water, and the level of the water noted. Shortly afterward the yellow of the egg will be seen rising in the tube, and the level of the water falling in the wine-glass. The water of the glass gradually passes through the

membrane of the egg, distending it, and forcing the contents of the egg upward. On the other hand, the salts of the egg—the chlorides, phosphates, sulphates—will be found to have diffused away from the rest of the egg into the water of the glass, as can be readily shown by appropriate tests. Thus, if a few drops of silver nitrate be added to the water, at once argentic chloride will be formed and precipitated, showing that the sodium chloride has passed into the water.

An important fact to be noted, the physiological significance of which will be appreciated shortly, is that little or no albumen is found in the water, scarcely a trace of it, if any, passing through the egg membrane, particularly if the water be distilled.<sup>1</sup> In this experiment also, as well as in the preceding one, the substances on either side of the membrane (in the case of the egg, most of them at least) diffused into each other. This, as we shall see in a moment, depends not only on the membrane

<sup>1</sup> Compare Mialhe: *Chimie appliqué à la physiologie*, etc., p. 130. Beclard: *Gaz. des Hopitaux*, 1851, p. 324.



being capable of imbibing both liquids, but also that the latter were miscible with each other. If a membranous septum, however, be used, which will imbibe only one of the liquids, that one alone will traverse the septum, will increase the volume of the other liquid if it is miscible with it, but there will be no exchange.

A convenient way of illustrating this, and also of showing that a liquid septum will act in this respect in the same way as a membranous one, is to place in a vial some chloroform, and then pour gently on the chloroform water, and on the top of the water sulphuric ether, the water serving as the septum. In a short time it will be found that the ether has passed through the water and has mixed with the chloroform, so that instead of the vial containing three layers, ether, water, and chloroform, it contains only two—water on top, and a mixture of chloroform and ether below. The chloroform having no affinity for the water, will not pass through it; the ether, on the other hand, will not only pass through the water, but, being miscible with the chloroform, will diffuse into it, and so give rise to the result just described. Osmosis further will take place, semi-liquid substances being used as septa. Thus, if sulphuric acid and litmus water be separated by boiled gelatin, the acid will make its way through the gelatin, and will color the litmus. The litmus, however, having but little affinity for the gelatin, diffuses but slightly into the gelatin, so that but little of the septum is colored.

Having given several illustrations of osmosis, let us consider now the causes of the same. The phenomenon of osmosis depends essentially upon two conditions: first, that the membranous septum is capable of imbibing the liquids which it separates; second, that the liquids are miscible. It will be remembered that in speaking of the organic proximate principles, allusion was made, among their other properties, to that of their taking or giving up of water. The swelling up of a tendon or muscle when immersed in water, and the giving up of the same when desiccated, are common examples of the imbibition by organic tissues of liquids. Every organic tissue and, indeed, all substances, however solid they may appear, are more or less porous, at least in the sense that the particles of which a body consist are separated to a greater or less extent from each other. It is through the presence of the interspaces, between the particles of which a tissue consists, that imbibition is possible, that the tissue is capable of taking up a liquid, retaining it for some time, and finally giving it up again.

The passage of a liquid into the interspaces or interstices of a tissue is, however, an example of capillarity, the particles of which the tissues consist bearing to the liquid passing through the spaces between them the same relation that the walls of a capillary tube bear to the liquid moving within them. The ascent of the oil in the wick of a lamp is a familiar example of capillary action.

Imbibition, the first condition of osmosis, depending as it does upon capillarity, necessitates, for its understanding, a brief consideration of this principle. Capillary attraction, so called on account of its being usually observed in tubes of very fine hair-like or capillary diameter,

can be best understood if we confine our attention for the moment to one or two elementary physical facts.

It is well known that if a drop of mercury be placed upon a perfectly clean plate of glass it rolls off and falls to the ground, its globular form being preserved, the particles of the mercury being held together through the force of cohesion, and its falling from the glass being due to the want of any adhesion between the two substances. On the other hand, if a drop of water be placed on a similar plate or glass, the water becomes flattened, adhering to the surface, and when the glass is tilted the water runs to the edge, leaving a wet line, but does not fall to the ground, sticking to the plate in spite of gravity, the water being retained by the glass through the force of adhesion. If the plate be first greased, then the drop of water will behave like the drop of mercury, and for the same reason, the water not adhering to grease falls like mercury to the ground. There are, therefore, two forces, that of cohesion and adhesion. Through the first the particles of a substance are held together or cohere; through the second, the particles of one substance are attracted by those of a dissimilar one, or adhere.

Let us modify the preceding experiment by partially immersing a clean glass plate in a vessel of water. It will now be noticed that the surface of the liquid in contact with the glass is slightly elevated, and that this elevation gradually diminishes until the level of the remaining liquid is reached. (Fig. 94.) It is very evident from what has just

FIG. 94.

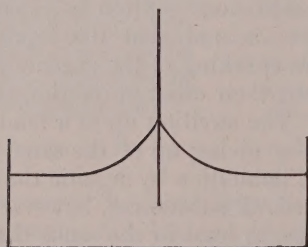
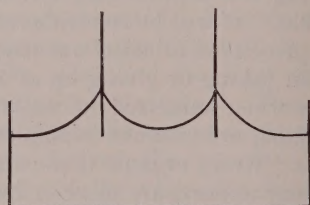


FIG. 95.



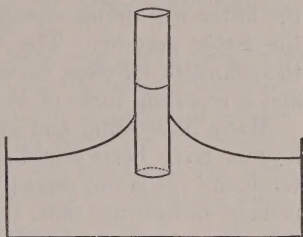
been said of adhesion and cohesion, that the different elevation of the water will be due to the relative strength of these two forces, the elevation of the liquid being highest where the liquid is in contact with the glass, adhesion being there at a maximum, cohesion at a minimum, and that the elevation will gradually diminish, the force of cohesion increasing, that of adhesion at the same time diminishing. Suppose, now, that we immerse a second plate of glass in the water parallel to the first, the water will be most elevated where the liquid comes in contact with the glass, the elevation diminishes as the distance from the second plate is increased, and the general surface of the water will be indicated by the curve (Fig. 95), the lowest point of the water being equidistant from the two glass plates. As the two glass plates are approximated, naturally the elevation of the water will be increased (Fig. 96), since the quantity of water being continually diminished, the



force of adhesion at the same time increases in proportion to the relatively greater surface of glass exposed. In a word, the elevation of the liquid is inversely as the distance of the plates.

If we now immerse two more plates of glass parallel to each other, and perpendicular to the first two, we shall have a four-sided glass arrangement, to the inside of which the water will adhere. The transition from such an apparatus to a capillary tube is, either theoretically or practically, a simple one, the conditions being in the latter essentially such as we have described.

FIG. 96.



Modern<sup>1</sup> theory deduces, then, the form and elevation of the liquid in capillary tubes as the resultant of the forces of adhesion, cohesion, and, of course, gravity. Inasmuch as these conditions are all present in the phenomena of imbibition, we are justified, as already observed, in regarding this an example of capillary action, the adjacent particles of a body being comparable to the plates of glass, or the side of a tube, the interspaces between them to the space between the plates, or within the tube, and the water to the liquid imbibed.

In order that an osmosis should take place, it is evident that the membranous septum must be not only capable of imbibing the liquids through capillary action, but further, that the liquids separated by the septum must be miscible, otherwise, though the liquids might get into the septum, they would not diffuse into one another, and there would be no current. This brings us, therefore, to the consideration of the second condition of osmosis, the diffusion of liquids.

It is a familiar fact that, if a drop of water rolling over a surface, upon which it can preserve its globular form, comes in contact with a drop of mercury, or of oil, the drops do not run into each other or fuse, the particles of the drop of water having a greater affinity for each other than for the particles of the drop of mercury or of oil, and *vice versa*. On the other hand, if the drop of water meets with a drop of alcohol, the two do run into each other, losing their identity, the particles of the water having a greater affinity for those of the alcohol than they have for each other. A simple illustration of the diffusion of liquids is to place in a small vial a solution of copper sulphate and immerse the vial containing the solution into a vase of water. Soon the surrounding water will assume a blue color through the diffusion into water of the copper.

The dissolving of a substance in a menstruum is an illustration of the same principle, the molecules of the dissolving liquid having a greater affinity for the particles of the substance to be dissolved than these have for each other. The solution of a substance, however, depends not only upon the affinities, chemical or physical, existing between the par-

<sup>1</sup> La Place : *Mecanique celeste* suppl. au livre x. *Euvres* t. iv. p. 389. Gauss : *Comment Soc. scient. Gott.*, vii. p. 39, 1829-1832. Ganot : *Physics*, transl. by Atkinson, p. 98. London, 1870. Weisbach : *Mechanics*, transl. by Cox, vol. i. p. 762. New York, 1872. Maxwell : *Theory of Heat*, p. 280. New York, 1877.

ticles of the substance and those of its menstruum, but also upon the fact that when the cohesive force holding together these particles ceases to act the particles become separated, repel each other, they acting then like the particles of a gas. Thus, if ice be dissolved by sulphuric acid, the latter will diffuse equally through the water, whatever the volume of the latter may be. The diffusion of liquids depends, therefore, upon the affinities existing between the particles of which the liquids consist and a repelling force of the same.

Many interesting and important facts in reference to the diffusion of liquids have been established, more particularly by the researches of Graham.<sup>1</sup> It is not essential, however, that we should dwell upon these, merely indicating that the diffusibility of liquids differs very much, according to their density, composition, the character of the septum, temperature, etc.

On account, however, of its important application to physiology it is necessary, before leaving the subject of diffusion, to call attention to the distinction made by Graham between what this physicist calls crystalloids and colloids, and which can be well illustrated by the following simple experiment: If a piece of potassium bichromate, or a little of the same substance in powder, be placed in the centre of a mass of boiled starch, in a few hours the whole of the starch will be seen colored, the potash having diffused through it. On the other hand, if a piece of caramel be similarly placed on a mass of boiled starch, it will remain where placed, not diffusing at all. Substances which diffuse readily, like the salts of potassium, are termed crystalloids, while those that do not do so are called colloids. Thus, in the experiment with the egg, the sodium chloride, being a crystalloid, diffuses through the egg membrane, while the albumen, being a colloid, remains within the egg. The method of dialysis of Graham, so useful as an instrument of analysis, is based upon this distinction of crystalloids: thus, if a fluid, consisting of a mixture of organic matter and arsenic, be placed in an endosmometer, in the course of twenty-four hours, perhaps, three-fourths of the arsenic will diffuse through the membrane into the surrounding water, the organic matters remaining within the jar. The application of the facts of capillarity and diffusion in the explanation of osmosis, as illustrated by the above experiments, is so evident, that it may appear superfluous to dwell further upon the subject. We will, therefore, merely call attention to the most important conditions.

In all the experiments which have just been described it is perfectly clear that the first condition of osmosis is that the liquid shall wet the membrane, or, in other words, that the membrane is capable of imbibition. This, we have seen, is due to capillary force. The second condition is, that the liquids having been imbibed by the membrane are miscible, or will diffuse, otherwise they would get no further than the interstices of the membrane, and there would be no currents. The modifications of the phenomena, according to whether the septum is solid, liquid, or semi-solid, as to whether the current is endosmotic or

<sup>1</sup> Phil. Trans., 1850



exosmotic, of the relative force of the two, etc., can be shown to depend upon these two conditions.

Having gone over this preliminary ground, let us now see whether the established facts of capillarity and diffusion, and the theory of osmosis deduced from them, can be applied to the explanation of absorption, as it takes place in the living body.

During absorption from the alimentary canal we have seen the digested food in a liquid or semi-liquid state pass through the epithelium, and the wall of a capillary or lymphatic into the blood or lymph. The epithelium and capillary wall in the living body are comparable, therefore, to the septum of the endosmometer, the liquids in the intestinal canal and the blood and lymph corresponding to the fluids separated by the septum in that instrument.

The action of a hydragogue cathartic, such as magnesium sulphate, is also an illustration of osmosis, since the salt passes from the interior of the alimentary canal through the epithelial layer of the intestine and wall of the capillary into the blood, and the watery part of the blood, together with some albumen (the latter effect being due, probably, to the presence of the saline), passes into the interior of the alimentary canal. The osmosis can be experimentally imitated by placing the solution of the magnesium sulphate within the jar of the endosmometer and the serum of the blood within the bulbous tube, the serum passing through the membrane into the magnesium sulphate, and the latter passing into the serum and increasing its volume.

Supposing that the jar represents the alimentary canal, and the bulbous tube the bloodvessel, the osmosis going on in the experiment is essentially the same as that in the living body after the administration of a hydragogue cathartic.

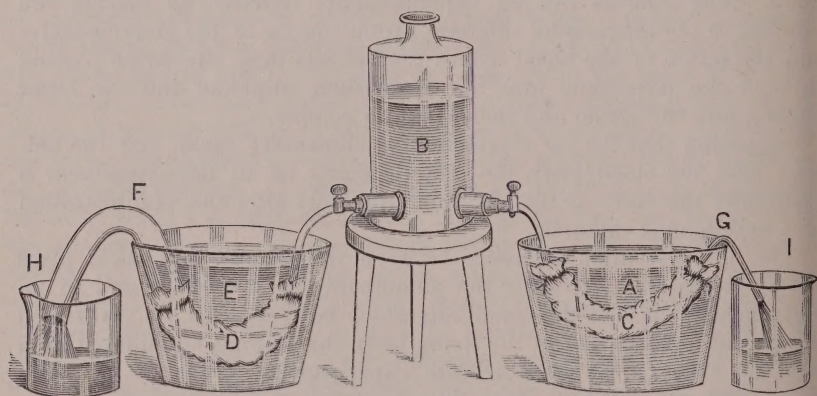
The only essential difference between the osmosis that takes place during absorption and after the administration of a saline and in an endosmometer is that the conditions which favor osmosis are realized in a way and to an extent in the living body that cannot be imitated for a moment, even in the most delicate experiments. Thus, it has been found that the activity of osmotic currents is in proportion to the extent and thinness of the membrane. When we come to study the capillary system we shall see that the extent of absorbing surface exposed by it is enormous, and that the walls of the capillaries are extremely delicate, measuring, on an average, perhaps from the  $\frac{1}{12000}$ th to the  $\frac{1}{25000}$ th of an inch in diameter.

One can readily imagine how favorable such a thin septum would be in the production of osmosis. It can be shown, also, as might have been supposed, that an endosmotic current is favored by having little or no pressure to overcome, such a current ceasing and beginning again, according as dense substances, like mercury, are added to or taken away from the fluid within the tube of the endosmometer. Now in the living body the pressure of the blood, even in the largest arteries, seldom exceeds six inches of mercury, and this pressure is very much reduced as the blood flows into the capillary and venous system, so that a current flowing from the intestine toward the blood meets with no very great resistance.

An important, though not indispensable, condition favoring the endosmotic current is the density of the solution in the bulbous tube of the endosmometer, the flow being usually greater according to the density of the solution. We find this to be the case, also, in absorption from the intestinal cavity, the endosmotic current being active in proportion to the amount of albumen and salts in the blood. Hence the activity of absorption after the administration of hydragogue cathartics, such drugs diminishing the watery constituents of the blood, and so increasing its density, while, at the same time, they diminish pressure. Again, osmotic currents are more active if the liquids are kept in movement. Thus, when osmosis has ceased, it can often be made to commence again by simply stirring the liquids. It is evident from this how great and favorable are the influences exerted by the circulation of the blood and lymph in promoting osmosis and absorption.

The importance of the movement of the liquids, or of one of them, in favoring osmosis is shown by the simple apparatus represented in Fig. 97. A jar (B), furnished with two stopcocks, is filled with a colored

FIG. 97.



fluid, litmus water, for example. To both stopcocks are fitted equal portions of intestine (D and C), which are immersed in the vases of water E and A. Into the piece of intestine C is fitted a siphon (G) of smaller diameter than that of the intestine, a siphon (F) of as large diameter being inserted into the piece of intestine D. Both siphons (F and G) pass into the vases H and I. The stopcocks of the reservoir (B) being opened, the colored fluid will flow into the two pieces of intestine, but inasmuch as the small size of the siphon G will offer an obstacle to the flow of the colored liquid through it into the vase I, the piece of the intestine G will become distended, and there will be an exosmosis from it of the colored fluid into the water of the vase A. On the other hand, the colored fluid passing readily through the siphon F, on account of its large size, the piece of intestine D will become flaccid, and there will be a rapid flow of the water of the vase E, through the intestine D, into the colored fluid flowing through it, or an endosmosis.



Finally, an increase of temperature promotes osmosis; the high temperature of the living body is, therefore, another favorable condition in producing this phenomenon. It is very probable, also, that electrical action may influence the production of osmotic currents in the living body, as we have seen to be the case in the experiments of Porrett. At present, however, no definite statement can be made as to the influence electricity may exert upon absorption.

It will be remembered that, in the experiment with the egg, attention was called to the fact that no albumen passed through the membrane from the egg into the water of the glass. So it is with the albumen of the blood, the flow of the contents of the intestine being toward the albumen of the blood, as the flow of the water is toward the albumen of the egg. Indeed, albumen is one of the most powerful of endosmotic substances. On the other hand, albuminose is readily absorbed by the bloodvessels; the significance of the conversion of albumen into albuminose by the gastric juice becomes now very evident.

The theory of absorption that we have just sketched is that almost universally accepted by physiologists, at least so far as concerns the absorption of albuminose, glucose, salts, water, etc.

There are, however, still differences of opinion as to whether the absorption of fats can be explained in this way. It seems to us that the want of success in demonstrating the passage of fats through membranes out of the body has often been due to the fact that the proper conditions for the success of the experiment were not realized.

It will be remembered that, during digestion, the fat is emulsified, and becomes mixed with the bile, alkaline fluids, etc., and that, during absorption, this modified fat passes into an alkaline fluid, the lymph. It is essential, therefore, that these conditions should be fulfilled if we wish to demonstrate the osmosis of fat out of the body. First, then, we must make an emulsion of fat, for example, by adding pancreatin to olive oil, and then make this distinctly alkaline by adding bile or a sodium salt. Place the alkaline emulsified fat in the jar of the endosmometer, making the water of the bulbous tube distinctly alkaline also, so as to resemble the alkaline lymph. If the water in the reservoir be examined some hours afterward, the fat will be found floating in drops upon the surface, it having osmosed through the membrane.

RÉSUMÉ.—We have seen that, as fast as the food is digested, it is absorbed, the albuminose, glucose, salts, and water being taken up by the radicles of the portal vein, the fats by the lymphatics of the small intestine, or the lacteals, often a small quantity of albuminose, etc., passing into the lymphatics, the portal vein taking up, also, occasionally, some fat, and that the absorption of food is an illustration of osmosis, the latter depending upon capillary attraction and the diffusion of liquids. Whichever of the two routes is taken by the digested food in absorption, the essential fact is that it gets into the blood sooner or later, and thence is carried by the circulation to all parts of the economy, repairing the waste of the tissues and supplying the fuel for the maintenance of the heat of the body and development of force.

The composition and circulation of the blood will be, naturally, then, the next subject for our consideration. To these, then, let us now turn.

## CHAPTER XIII.

### THE BLOOD.

From time immemorial the blood has been recognized as the most important fluid in the human body, as well as in that of animals—indeed, as indispensable to life. Daily observation continually shows that its loss prostrates the body and enfeebles its powers, and, with excessive hemorrhage, that life itself ebbs away,

“For the life of the flesh is in the blood.”

This is readily understood when it is known that the blood circulating through the economy is the source of the animal heat, and carries to the tissues, and the cells composing them, material for their growth, renewal, and repair, and, at the same time, removes from them that which has become effete and worn out in producing the phenomena of life.

This “peculiar juice,” as the Mephistopheles of Goethe calls it, represents, therefore, the life of the day, of the past, and of the morrow. Let us consider first its physical characteristics.

The blood is an alkaline fluid, with a specific gravity, when defibrinated, according to Becquerel and Rodier,<sup>1</sup> of from 1.055 to 1.063. The opacity of the blood is due to the fact that it is not a homogeneous liquid, being composed, as we shall see presently, of two elements—corpuscles and liquor sanguinis, or plasma; these, differing in their refractive power, offer an obstacle to the transmission of light, which is lost in its passage from the air through the liquor and corpuscles. The blood has a saltish taste, and a faint but distinct odor. This becomes more apparent when a few drops of sulphuric acid are added to the specimen examined. It may be mentioned, in this connection, that the importance of the odor of the blood, as made use of in criminal cases, and often insisted upon by medico-legal writers, has been grossly exaggerated.

The temperature of the blood in man, so far as is known, varies from 80° to 100° Fahr., but it is very probable that, in certain parts of the body, it is several degrees higher. Bernard found that in dogs and sheep the temperature in the aorta ranged from 99° to 105°, and reached even 107° in the hepatic vein. According to the same authority, the blood is hotter in the right than in the left side of the heart; the temperature is higher in the arteries than in the veins, with the exception, however, of the blood in the portal vein, which is warmer than that in the aorta independently of digestion.<sup>2</sup> The sudden rise of temperature often observed in man just before death, due, perhaps, to the loss of vascular tonicity, would seem to show that the temperature

<sup>1</sup> *Traité de Chimie Pathologique*, p. 95. Paris, 1854.

<sup>2</sup> *Sur les Liquides de l'Organisme*, tome i., 3d, 4th, 5th leçons.



of the blood in the deeper vessels in man is as high as that observed by Bernard in the animal just mentioned.

One of the most striking features of the blood is its color, red or scarlet in the arteries, blue or black in the veins. As first demonstrated by Lower,<sup>1</sup> this difference is due to the venous blood absorbing air as it passes through the lungs. When we come to study the circulation and respiration, we shall see that, as the red blood passes through the capillaries it loses oxygen and gains carbonic acid, becoming blue, while it turns again into red blood in the lungs with the fresh absorption of oxygen. The blood of the pulmonary artery, however, is blue, while that of the pulmonary vein is red. The blood in the veins coming from glands, during secretion, as shown by Bernard,<sup>2</sup> is also red, and this is the case also in the veins when the sympathetic is cut. The explanation in these cases seems to be that the increased supply of arterial blood to the parts carries an excess of oxygen to the veins sufficient to maintain the red color of the blood flowing into them.

The brightness in color of the blood depends, to a certain extent, upon the form of the corpuscles; it is bright when they are flattened and hollowed, containing oxygen, and dark when they are distended and round, containing carbonic acid, the reflection of the light depending on the form of the corpuscles.

Numerous experiments have been made from time to time to determine, if possible, the quantity of blood in the human body. Among others may be mentioned those of Valentin, Blake, Lehmann, and Weber. Valentin's method<sup>3</sup> consisted in injecting into the circulation of an animal a given quantity of a saline solution and then drawing some blood, estimating by evaporation the proportion of the water to the blood, and then comparing the excess of water with that of a quantity of blood drawn previously. Suppose that the excess of water in the specimen drawn after the saline injection was one part of water to ten of blood, and that five ounces of water had been injected, then the quantity of blood would be fifty ounces.

Blake<sup>4</sup> experimented by injecting sulphate of aluminium and then ascertaining the amount of the sulphate in a given quantity of blood drawn, arguing that the whole quantity of the sulphate injected was to that in the specimen drawn as the whole quantity of blood in the body was to that drawn.

The observations of Lehmann<sup>5</sup> and Weber were made upon two criminals who were first weighed and then decapitated. The blood remaining in the vessels after decapitation was calculated by injecting water into the vessels of the head and trunk until that which passed out by the veins exhibited only a pale yellowish color. This was evaporated and the dry residue was assumed to represent a certain quantity of blood, the ratio of blood to its residue having been previously ascertained. The amount of blood lost by decapitation was a little over twelve pounds, and that estimated by the above method as remaining

<sup>1</sup> Tractatus de Corde item de Motu et Colore Sanguinis, p. 180. Amstelodami, 1669.

<sup>2</sup> Op cit., pp. 268, 299.

<sup>3</sup> Repertorium für Anat. und Phys., 1837, Band ii. S. 281.

<sup>4</sup> Philadelphia Medical Examiner, August, 1849.

<sup>5</sup> Lehrbuch der Phys. Chemie, 1852, tome ii. S. 234.

in the vessels as a little over four pounds, making for the whole body 16.59 pounds.

TABLE XL.<sup>1</sup>—AMOUNT OF BLOOD IN THE BODY.

|         |                                            |
|---------|--------------------------------------------|
| 12 lbs. | of blood lost in execution.                |
| 4 "     | of blood collected by washing.             |
| 16 "    | of blood in criminal weighing 128 lbs., or |
| 1 "     | of blood to 8 of body weight.              |

The weight of one of the criminals was 132.7 pounds; this would give a ratio of about one pound of blood to every eight of body, which is about what physiologists generally assume. It must be remembered, however, that this is only an approximation, for the amount of blood left in the body after decapitation cannot be accurately determined by the method just mentioned. Further, the amount of blood in the body is notably increased during digestion. Bernard<sup>2</sup> has shown that an animal like the rabbit, for example, during digestion can lose twice as much blood as when fasting. Burdach<sup>3</sup> refers to a case reported by Wrisberg of a woman losing over twenty-one pounds of blood after decapitation. Facts like these show the importance of taking into consideration the state of the system in determining the quantity of blood. In a general way this may be stated in an adult healthy man to amount to sixteen or twenty pounds and is distributed, according to Ranke,<sup>4</sup> in round numbers as follows:

|                                |                                 |
|--------------------------------|---------------------------------|
| $\frac{1}{4}$ vascular system. | $\frac{1}{4}$ skeletal muscles. |
| $\frac{1}{4}$ liver.           | $\frac{1}{4}$ remaining organs. |

When the blood is examined under the microscope, for example, circulating in the web of a living frog's foot, it will be seen to consist, as already mentioned, of two distinct portions, a transparent colorless liquid, the liquor sanguinis or plasma, and of minute bodies or corpuscles, the blood globules or blood cells. These corpuscles, which float in the liquid part of the blood, are of two kinds, the white and the red. The latter, discovered by Leuwenhoek<sup>5</sup> in 1673, are far more numerous than the former and give to the blood its red color, they being carriers of oxygen.

Let us study the red corpuscles first and then the white, reserving for the present the consideration of the plasma.

When blood is examined under the microscope the corpuscles will be observed in different positions, some on their edges or sides, others lying flat (Fig. 98). It can be seen that they are circular, flattened disks, about four times as broad as thick and biconcave in form. From this latter circumstance they are thinnest in the centre. Therefore, when a corpuscle is viewed under the microscope from the flat side, if the edges are in focus the centre will appear dark, simulating a nucleus (Fig. 99); whereas, when the centre is in focus and is light the edges will appear dark (Fig. 100). In reality, however, there is neither a nucleus nor a membranous cell-wall, the red corpuscle being a homogeneous structure-

<sup>1</sup> Lehmann, op. cit.

<sup>2</sup> Op. cit., tome i, p. 419.

<sup>3</sup> *Traité de Physiologie* traduit, par Jourdain, tome vi, p. 116. Paris, 1837.

<sup>4</sup> *Physiologie*, 1871, S. 373.

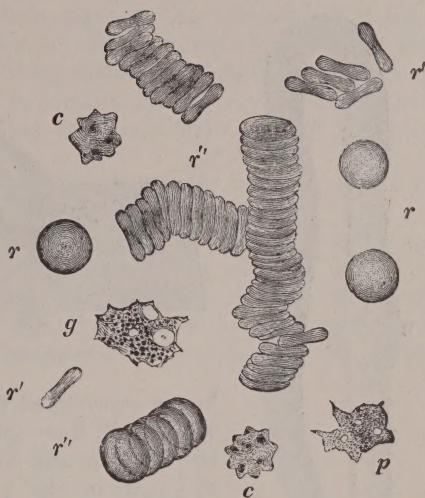
<sup>5</sup> *Philos. Transactions*, p. 23. London, 1674.



less mass of living matter, soft, transparent, elastic, and of a pale amber color. The red color of the blood is due to the immense number of the corpuscles. Vierordt<sup>1</sup> estimates that a cubic millimetre in the male contains 5,000,000, in the female 4,500,000.

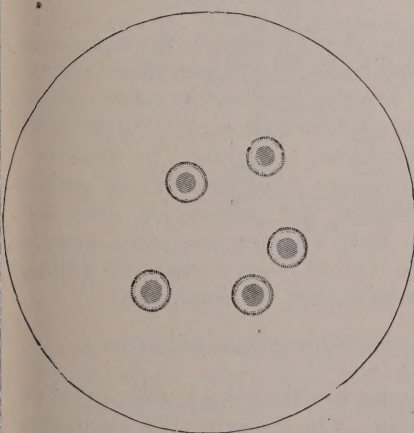
The method we make use of in counting the blood corpuscles is essentially that of Malassez and Potain<sup>2</sup> and Gowers.<sup>3</sup> It consists in sucking up into a graduated tube (Fig. 101, A) one cubic millimetre ( $\frac{1}{25}$ th of an inch) of blood and then a five per cent. solution of sodium chloride from a jar into the tube until the blood and the solution are drawn into and fill the dilated portion (Fig. 101, B) of the tube. This dilated portion having a capacity of 100 millimetres, the blood will then be diluted 100 times. One millimetre of this mixture will, therefore, contain the  $\frac{1}{100}$ th of a millimetre of blood and the  $\frac{1}{100}$ th of a millimetre of the mixture  $\frac{1}{100}$ th of  $\frac{1}{100}$ th or the  $\frac{1}{10000}$ th of a millimetre of blood. This mixture of blood and salt solution is then forced out on an object glass

FIG. 98.



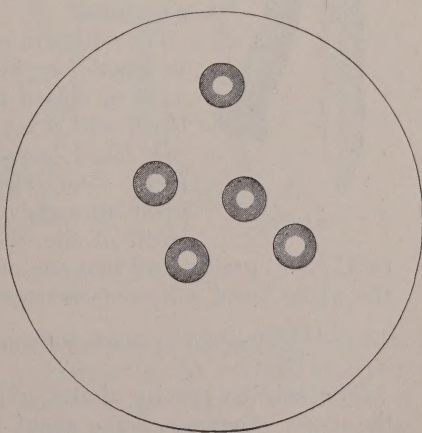
Human blood as seen on the warm stage. Magnified about 1200 diameters. *c, c.* Crenate red corpuscles. *p.* A finely granular. *g.* A coarsely granular pale corpuscle. Both exhibit two or three vacuoles. In *g* a nucleus also is visible. (QUAIN.)

FIG. 99.



Red globules of the blood, seen a little beyond the focus of the microscope. (DALTON.)

FIG. 100.



The same, seen a little within the focus. (DALTON.)

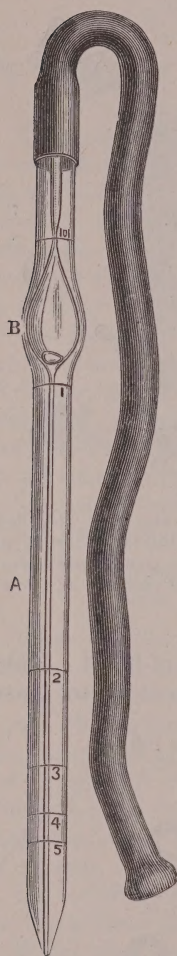
<sup>1</sup> Physiologie, S. 9. Tubingen, 1871.

<sup>2</sup> Archiv de Physiologie, p. 32. Paris, 1876.

<sup>3</sup> Lancet, 1877, p. 797.

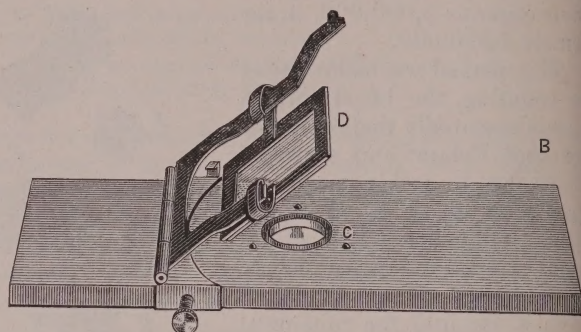
(Fig. 102, C) which under the microscope is seen to be divided into ten squares, each of which when covered by the compressorium (Fig. 102, D)

FIG. 101.



Mixer.

FIG. 102.



Graduated moist chamber with compressorium.

has a capacity of the  $\frac{1}{100}$ th of a millimetre. Each square will then contain the  $\frac{1}{100}$ th of a millimetre of the mixture, and consequently will contain the  $\frac{1}{100}$ th of  $\frac{1}{100}$ th or the  $\frac{1}{10000}$ th of a millimetre of blood. Further, it will be noticed that each square (D) is subdivided into twenty smaller squares, the object of which is to facilitate the counting of the corpuscles. Suppose now, for example, that twenty-five corpuscles could be counted on each of the small squares, then the large square would contain 500 corpuscles; but as the large square contains only the  $\frac{1}{10000}$ th of a millimetre of blood, it follows that one cubic millimetre ( $\frac{1}{25}$ th of an inch) will contain  $500 \times 10,000$ , or 5,000,000 corpuscles.

The division of the object glass into ten squares is to enable one to make ten independent observations, so as to obtain an average result. A cubic inch of blood will contain, therefore, over 70,000,000,000 red blood-corpuscles, or, according to Huxley,<sup>1</sup> more than eighty times the number of people upon the globe, or on the supposition that the blood of the whole body amounts to sixteen pounds or 112,000 grains, and that one cubic inch of blood weighs 168 grains, the whole blood will contain over forty trillion red corpuscles.

$$\frac{112000}{168} = 607 \times 70,000,000,000 = 40,000,000,000,000 \text{ corpuscles.}$$

The specific gravity of the corpuscles is a little higher than that of the liquor sanguinis, being about 1.085. On observing the corpuscles in blood removed from the body, it will be noticed that soon a number of them run together, forming a chain-like rouleaux of coin (Fig. 98).

<sup>1</sup> Elementary Physiology, London, 3d ed., p. 78.

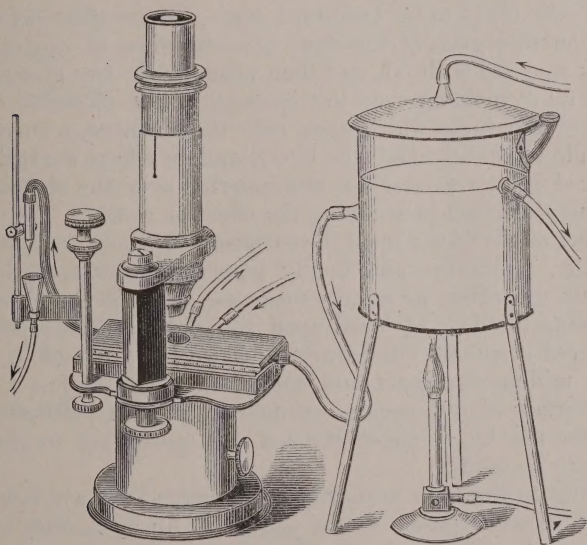


This is due, according to Robin,<sup>1</sup> to an exudation from the corpuscles themselves which causes them to adhere to each other. Shortly after the blood is drawn the corpuscles will exhibit also small prominences on their surfaces, giving them a raspberry-like appearance, and as they become dry they shrivel up and their edges become crenated (Fig. 98). The shape of the corpuscles, however, can be restored even after the lapse of months and years by treating them with a fluid of the density of serum (1.028). This fact is important, from a medico-legal point of view, in reference to determining whether a stain upon clothing or floors, etc., is blood.

The corpuscles swell up and dissolve when pure water is added to them, and acetic acid and other acids have the same effect.

Under the influence of alkalies the corpuscles instantly swell up, appear to burst, and then entirely disappear. The effect of heat is to produce in them bud-like processes. In studying the effects of such reagents as those just mentioned, as well as others, the apparatus represented in Fig. 103, which is to be placed on the stage of the micro-

FIG. 103.



Stricker's warm stage.

scope, will be found useful. It consists of a brass box opening laterally by two tubes, with a solid rod-like projection in the middle, and perforated in the centre. The central aperture can be converted into a chamber by cementing to its lower opening a cover glass. Surrounding this central chamber is coiled the bulb of a thermometer, whose registering surface is attached externally to the side of the box.

<sup>1</sup> Journal de la Physiologie, tome i. p. 295. Paris, 1858.

By connecting one of the lateral apertures opposite the projecting rod of the box with the reservoir of hot water and the other with a waste pipe a constant flow of hot water through the brass box is insured, and the temperature of the central chamber regulated as desired by the thermometer.

By screwing on to the rod-like projection of the brass box a rod of the same metal and heating its free end by a spirit lamp, the temperature can also be elevated as required.

If it is desired to study the action of water upon the blood corpuscles, for example, the apparatus is used in the following way: A drop of water is placed on the floor of the chamber, and a drop of blood, usually diluted with salt solution, upon a cover-glass; the latter is then placed inverted over the chamber, the edges of which have been previously oiled or surrounded with a ring of putty, so as to make the chamber air-tight. By allowing the hot water to flow through the brass box, or heating the end of the rod by the spirit lamp, the drop of water on the floor of the chamber is made to evaporate, and, condensing on the under surface of the cover-glass, gradually affects the blood-corpuscle it meets there.

The effects of heat simply upon the blood corpuscles can be studied by placing the blood to be examined upon a cover-glass, and dropping this upon another glass of the same size, the edges of which have been previously smeared with oil, and then placing the two glasses with the blood and oil so inclosed over the opening of the chamber. Further, by means of the tubes which open into the chamber, a current of gas can be made to pass through the latter, and its effects studied upon the blood placed upon a cover-glass and inverted over the chamber, in the manner just described in studying the effect of water.

The effect of electricity upon the corpuscle is to convert it temporarily into rosette-, mulberry-, and finally horsechestnut-shaped forms. To demonstrate this effect, we usually make use of the electrical microscopic stage, placing the drop of blood upon the slide in such a position that when covered it spreads out between the two poles of tinfoil, which are about six millimetres apart and connected either with a Leyden jar having a surface of 500 square centimetres, or by a Du Bois-Reymond inductorium fed by a single Bunsen cell, according to the kind of electricity to be used.

According to the high authority of Gulliver,<sup>1</sup> the average diameter of the red blood-corpuscle is the  $\frac{1}{3200}$ -th of an inch, with an average thickness of about the  $\frac{1}{12400}$ -th of an inch. The diameter, however, varies as much as from the  $\frac{1}{2800}$ -th to the  $\frac{1}{4000}$ -th of an inch. The importance of remembering these variations will be seen presently.

<sup>1</sup> In Works of William Hewson, Sydenham edition, p. 237. London, 1846.



TABLE XLI.<sup>1</sup>—BLOOD CORPUSCLES.

| <i>Mammals.</i>           |  |  |  |                   |             |
|---------------------------|--|--|--|-------------------|-------------|
| Animal.                   |  |  |  | Diameter.         |             |
| Manatee . . . . .         |  |  |  | $\frac{1}{2700}$  | of an inch. |
| Elephant . . . . .        |  |  |  | $\frac{1}{2745}$  | " "         |
| Ant-eater . . . . .       |  |  |  | $\frac{1}{2769}$  | " "         |
| Sloth . . . . .           |  |  |  | $\frac{1}{2865}$  | " "         |
| Whale . . . . .           |  |  |  | $\frac{1}{3099}$  | " "         |
| Camel . . . . .           |  |  |  | $\frac{1}{3123}$  | " "         |
| Man . . . . .             |  |  |  | $\frac{1}{3200}$  | " "         |
| Orang . . . . .           |  |  |  | $\frac{1}{3383}$  | " "         |
| Chimpanzee . . . . .      |  |  |  | $\frac{1}{3412}$  | " "         |
| Dog . . . . .             |  |  |  | $\frac{1}{3542}$  | " "         |
| Opossum . . . . .         |  |  |  | $\frac{1}{3557}$  | " "         |
| Rabbit . . . . .          |  |  |  | $\frac{1}{3607}$  | " "         |
| Black Rat . . . . .       |  |  |  | $\frac{1}{3754}$  | " "         |
| Mouse . . . . .           |  |  |  | $\frac{1}{3814}$  | " "         |
| Brown Rat . . . . .       |  |  |  | $\frac{1}{3911}$  | " "         |
| Gray Squirrel . . . . .   |  |  |  | $\frac{1}{4000}$  | " "         |
| Ox . . . . .              |  |  |  | $\frac{1}{4267}$  | " "         |
| Cat . . . . .             |  |  |  | $\frac{1}{4404}$  | " "         |
| Sheep . . . . .           |  |  |  | $\frac{1}{5300}$  | " "         |
| Goat . . . . .            |  |  |  | $\frac{1}{6366}$  | " "         |
| Pigmy Musk Deer . . . . . |  |  |  | $\frac{1}{12325}$ | " "         |
| <i>Birds.</i>             |  |  |  |                   |             |
| Ostrich . . . . .         |  |  |  | $\frac{1}{1649}$  | " "         |
| Owl . . . . .             |  |  |  | $\frac{1}{1763}$  | " "         |
| Swan . . . . .            |  |  |  | $\frac{1}{1806}$  | " "         |
| Pigeon . . . . .          |  |  |  | $\frac{1}{1973}$  | " "         |
| <i>Reptiles.</i>          |  |  |  |                   |             |
| Turtle . . . . .          |  |  |  | $\frac{1}{1231}$  | " "         |
| Viper . . . . .           |  |  |  | $\frac{1}{1274}$  | " "         |
| Lizard . . . . .          |  |  |  | $\frac{1}{1555}$  | " "         |

<sup>1</sup> Drawn up principally from table of Gulliver, op. cit., p. 237, and observations of author.

| <i>Amphibia.</i>   |  |                  |             |
|--------------------|--|------------------|-------------|
| Animal.            |  | Diameter.        |             |
| Amphiuma . . . . . |  | $\frac{1}{363}$  | of an inch. |
| Proteus . . . . .  |  | $\frac{1}{400}$  | " "         |
| Siren . . . . .    |  | $\frac{1}{429}$  | " "         |
| Menopoma . . . . . |  | $\frac{1}{563}$  | " "         |
| <i>Fishes.</i>     |  |                  |             |
| Pike . . . . .     |  | $\frac{1}{2000}$ | " "         |
| Perch . . . . .    |  | $\frac{1}{20}$   | " "         |
| Lamprey . . . . .  |  | $\frac{1}{2134}$ | " "         |

While there is not always a proportional relation between the size of the blood corpuscle and that of the animal—that of the ox, for example, being smaller than that of man or the dog (Table XLI.)—Milne Edwards<sup>1</sup> has shown by a comparison of the size of the blood corpuscle in the five classes of vertebrates, that there does exist a most remarkable connection between the size of the corpuscle and the degree of nervo-muscular power of the animal; the corpuscles being small in the most highly developed and active vertebrates, and large in those least so. It will be seen also, more particularly, that the size of the corpuscle is most intimately related to the activity of the respiration, the corpuscle being smallest in those animals whose respiration is the most active, and largest in those in which this function is slow. This might be expected, as a large number of small corpuscles offer a larger absorbing surface to the oxygen, the respiratory element, than a small number of large ones. As we proceed we shall see that muscular is largely dependent upon respiratory activity. Hence, if the above view be correct, we should expect to find the blood corpuscles smallest in the active vertebrates and largest in the sluggish ones.

On comparing the size of the blood corpuscles in the mammalia with those of the reptilia or batrachia (Table XLI.), we find such to be the case. Of course, if this comparison be carried out to extreme detail, there will be found exceptions to the rule, for no doubt other conditions beside those of respiration influence the size of the corpuscles, possibly the character of the food, etc.; but that the connection just referred to is something more than mere coincidence seems to be fully justified by Milne Edwards's elaborate survey of the facts.

It will be seen from Table XLI. that there are a few mammals in which the blood corpuscles are larger than those of man, and that the blood corpuscle of the pigmy deer (*Tragulus*) is the smallest known, while those of a batrachian, the amphiuma, are the largest.

The exact size of the red blood-corpuscle in man is not only of interest physiologically, but also from a medico-legal point of view. Attention has already been called to the fact that there is a considerable variation in the size of the human corpuscles, and hence it is often impossible to say positively whether a given corpuscle came from a human being's blood or that of an ape, dog, rabbit, rat, mouse, or ox,

<sup>1</sup> Physiologie, tome i. p. 57.

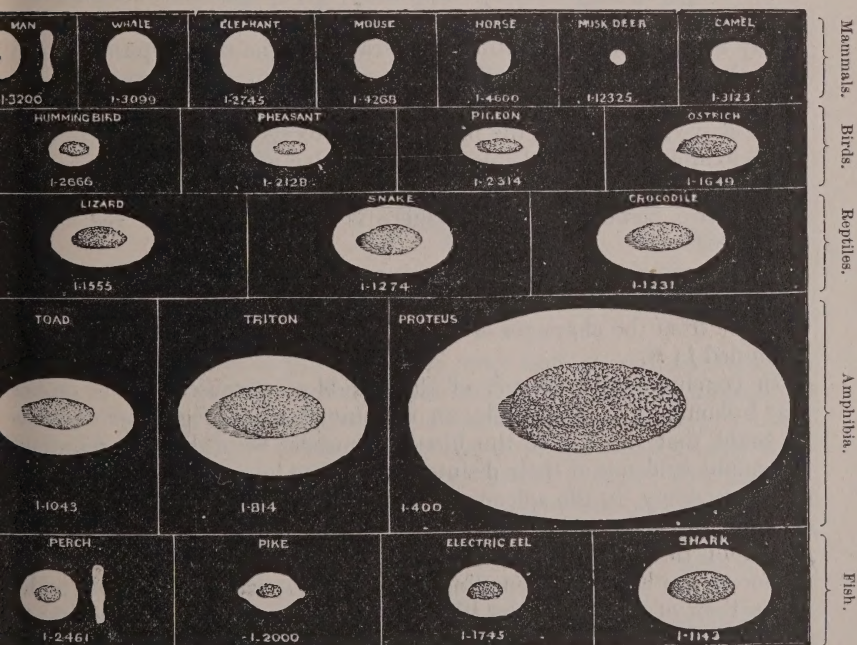


for the average diameter of the corpuscles in these animals is within the limits of the variations that have been mentioned as occurring in man.

When a large quantity of human blood is examined, probably ninety-five corpuscles out of every hundred will exhibit the same diameter, but in a medico-legal investigation the amount of blood put at the disposal of the expert is often exceedingly small—an old blood-stain, a single drop, perhaps, and possibly the variable corpuscles contained in this very drop. Now, as the size of the corpuscle in the dog or the ox varies as well as that of man, if the size of the corpuscle in the suspected fluid is only taken into consideration, the blood of a dog might be determined to be that of a man, and *vice versa*. In fact, it is impossible to say beyond the shadow of a doubt that a given drop of liquid is human blood and not that of the animals referred to above, for the small size of the variable human corpuscle might lead the examiner to think the human blood had come from a dog or a mouse, while from the variable large corpuscles in the blood of these animals there might be a suspicion that their blood was human.

With the exception of the camel and llama, in which the red blood-corpuscles are oval, the form of these bodies in the mammalia thus far examined is circular, which adds to the difficulty of distinguishing the

FIG. 104.



Typical character of red blood-cells of vertebrata. (KIRKES.)

blood of the domestic mammals from that of man. On looking at Fig. 104, it will be seen that the red blood-corpuscles in birds, reptiles, batrachia, and fishes differ from those of man and the mammalia gener-

ally in being oval in form and in exhibiting a well-marked nucleus, and in being much larger.

The only partial exceptions to the above statement are offered by the oval corpuscles of the dromedary and llama; but, as will be seen from Fig. 104, they are not nucleated. At the other end of the vertebrate series we find a further exception, in the nearly circular corpuscles of the lamprey, but these are nucleated. There can be no difficulty, therefore, in distinguishing the blood corpuscles of the birds, reptiles, etc., from those of mammals. The oval form, and the presence of a nucleus, especially, are sufficient to decide positively that the blood containing such corpuscles is not mammalian. Such knowledge has been of advantage more than once in assisting in the detection of murder.

The most important use of the red blood-corpuscles is undoubtedly as carriers of oxygen. Blood will absorb ten to thirteen times as much oxygen as water, and this property depends upon the corpuscles. In addition to the facts already referred to of the connection between the respiratory power and the corpuscles, it may be mentioned that the number of corpuscles is greater in the active carnivora than in the more sluggish herbivora, and that in man in those individuals whose nervo-muscular energies are most developed we find the greatest number of corpuscles, whereas in the anæmic the number falls below the standard.

Vital activity of all kinds, respiratory, nervo-muscular, etc., necessitates a constant and free supply of oxygen, and this want is preëminently filled by the circulating blood carrying the red corpuscles laden with the indispensable element. Even apparent exceptions, like the absence of the red corpuscles in insects offers, are really no exceptions to the above statement of the importance of oxygen, for in those animals which exhibit such remarkable nervo-muscular power the oxygen is carried directly to the tissues by the tracheal system of tubes permeating their entire bodies, and hence there is no necessity for red blood-corpuscles.

In the remaining vertebrata the amount of carbonic acid and heat produced and nervo-muscular power put forth are about what might be expected from the character of their blood and the corpuscular elements contained in it.

In concluding this sketch of the red blood-corpuscles, it is proper that I should give, if possible, an account of their origin, for there is no doubt that the life of the blood corpuscles is of limited duration. Abundant evidence of their disintegration is to be seen in different parts of the economy, in the spleen and in the liver for example, in the form of blood crystals, and, as we have seen, in speaking of the coloring matter of the bile, that the bilirubin is polymeric with the coloring matter of the blood or hæmatin, it is probable that the bilirubin is developed out of the corpuscles disintegrated in the liver. According to some physiologists, the origin of the red corpuscles is entirely unknown, while it is held by others that they are developed in some way out of the white corpuscles of the blood. To appreciate the facts brought forward in favor of the view that the red corpuscles are modified white ones, it will be first necessary to describe the latter, which up to this time have been only incidentally alluded to.

To the consideration of the white corpuscles let us now turn.



## CHAPTER XIV.

### THE BLOOD.—(*Continued.*)

THE white corpuscles discovered by Hewson<sup>1</sup> about 1770, as their name implies, are of a grayish, whitish color, of a round form, and consist of a mass of protoplasm containing granules. A cell wall cannot be said to exist. Chemically the white corpuscles are composed of albuminous substances, lecithin, glycogen, salts.<sup>2</sup>

When the blood is maintained at the temperature of the body the form of the white corpuscle is seen to be constantly changing, alternately protruding and retracting its body substance in an amœbiform manner (Fig. 105). By adding finely powdered indigo to serum containing

FIG. 105.



Various forms assumed by the white corpuscles of the blood. The upper row represents the white corpuscles of man; the lower row, white corpuscles from the newt, showing changes effected in fifteen minutes. (CARPENTER.)

white corpuscles the manner in which they feed can be observed, the indigo being drawn into the body of the corpuscle by the retraction of its amœba-like arms and then gradually absorbed and assimilated. Under the influence of acetic acid the body of the corpuscle clears up and three or more nuclei appear. Whether these nuclei preëxist and the acid only makes them apparent, or whether their appearance is due to a kind of coagulation, has not yet been positively determined. By the continued action of water and acetic acid, and more readily by alkalies, the white corpuscles are dissolved and disappear.

The white corpuscle is larger than the red one, measuring on an average the  $\frac{1}{2500}$ th of an inch. The white corpuscles are far less numerous than the red ones, being found usually in the proportion of one white corpuscle to between 300 and 500 red ones. This proportion as we learn, however, from the observations of Hirst,<sup>3</sup> varies according to the state

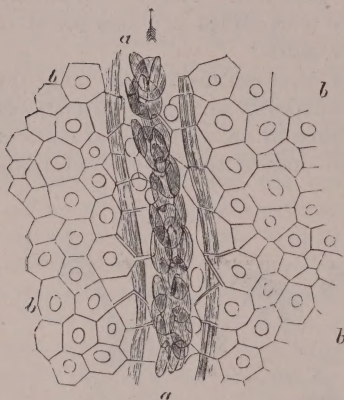
<sup>1</sup> Works, p. 282.

<sup>3</sup> Muller's Archiv, 1856, p. 174.

<sup>2</sup> Hoppe-Seyler: Untersuchungen, Band iv. S. 441.

of digestion: thus before breakfast the proportion being about 1 to 1800, one hour after breakfast it was 1 to 700, before dinner 1 to 1500 after dinner, 1 o'clock, 1 to 400, two hours later 1 to 1475, after supper, 8 P. M., 1 to 550, at midnight about 1 to 1200. The white corpuscles differ also in many other respects from the red ones: thus in the manner in which they are affected by various reagents, and in the way in which they adhere to the walls of the vessels in which they are circulating (Fig. 106), the red corpuscles keeping in the middle of the stream. The

FIG. 106.



A small venous trunk, *a*, from the web of the frog's foot. *b, b*. Cells of pavement-epithelium, containing nuclei. *d*. White corpuscles. *e*. Red corpuscles (CARPENTER.)

white corpuscles further are found in lymph, chyle, pus, and other fluids as well as in the blood; the more general name of leucocytes is often, therefore, given to them.

It is well known that the leucocytes are most numerous in the splenic vein, and that in diseases of the spleen, liver, and lymphatic glands, the white corpuscles may increase in number to such an extent as to form a half or a third of the corpuscular part of the blood, hence the light color of the blood in such circumstances, and the name of the disease—leucocythemia.

The number of the white corpuscles increases in pregnancy, and are more numerous in children than in adults. The proportion of the white corpuscles to the red is far higher

in the embryo vertebrate than in the adult; according to Gulliver,<sup>1</sup> in the very early stages of embryonic life the white corpuscles are even in excess. Further, in examining the blood of the amphioxus, the simplest of vertebrates, and that of the invertebrata (with but few exceptions) one cannot but be impressed with the likeness of their corpuscles to the white ones of the vertebrates rather than to the red. Let us see whether these facts have any significance in throwing light upon the origin of the red and white corpuscles.

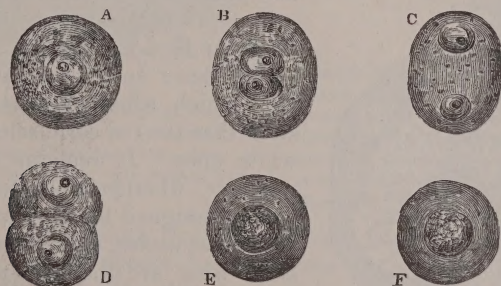
One of the most profound truths in the whole range of biology is that the transitory stages through which the higher animals pass are permanently retained in the lower ones. Ample evidence of the truth of this assertion will be given in the consideration of the phenomena of reproduction, and it will be found then that the blood does not offer any exception. If the red corpuscles are then modified white ones more highly developed, we should expect to find white corpuscles in the lower animals and in the embryonic forms of the higher, and that gradually the white ones should give way to the red as development advances. This we have seen is the case. Again, the white corpuscles are identical with those of the lymph and chyle, and as was pointed out it has long been a matter of comment that in the upper part of the thoracic duct

<sup>1</sup> Carpenter's Physiology, p. 234. London, 1881.



its fluid becomes of a reddish hue, due probably to the gradual development of the red blood-corpuscles. Again, the immense number of white corpuscles in the disease leucocythemia, just referred to, may be accounted for on the supposition that the abnormal conditions are such as to interfere with the normal transformation of the white corpuscles into the red. Another significant fact is that transitional forms between the red and the white corpuscles are often met with in the blood. These facts of comparative anatomy, embryology, and pathology, have a significance if this view of the transformation of the white corpuscles into the red be correct, otherwise they are meaningless. It must be admitted, however, that the exact manner in which the red corpuscle is developed from the white has not been definitely made out, although, according to Kuss,<sup>1</sup> both Kölliker and Recklinghausen have seen the transformation of white globules into red even outside the organism in blood kept at the temperature of the living organism in contact with a moist atmosphere. If it be admitted that the red corpuscle is developed from the white, the next question that will naturally be asked is, Where does the white corpuscle come from? In examining the blood corpuscles at different periods of embryonic life it will be found that some have a different origin from others. The first blood corpuscles are almost indistinguishable from the cells of the body of the embryo generally. When we come to study the development of the vascular system we shall see that, in the pellucid area of the embryo of the cells forming the mesoblastic layer some soften down and liquefy, while others remain floating in the liquor so produced. The latter are the first blood-cells or corpuscles; they are round, nucleated, and colorless, and reproduce themselves by fission. (Fig. 107.)

FIG. 107.



Reproduction of first blood corpuscles, in embryo, by fission. (KIRKES.)

With the development of the liver and spleen white corpuscles appear in the blood; the latter as they pass through the liver become colored, gradually they lose their granular appearance and become nucleated red blood-corpuscles, often oval shaped, which form, as we have seen, is retained through life in the oviparous vertebrates, but in the mammalia, with the exception of the camel tribe, is only transitory. Gradually the number of the white corpuscles diminishes, the red unnucleated biconcave corpuscles simultaneously increasing, the latter being wanting at the first month of intrauterine life, and at the third month constituting only about one-fourth of the corpuscles. With the development of the

<sup>1</sup> Physiology, translated by Dr. Amory, p. 122. Boston, 1875.

embryo the white corpuscles still further diminish, until, finally, the circular, biconcave, unnucleated red corpuscles predominate in the proportion already mentioned. Possibly the red corpuscles reproduce themselves also, to a certain extent, fissiparously—that is, by a process of division, in the adult as well as in the embryonic condition.

In certain cases after excessive hemorrhage the corpuscles may possibly be regenerated in this manner; for it is well known that many vegetable organisms reproduce themselves fissiparously in vast numbers, even in a night, far more rapidly than would be necessary in the case of the corpuscles, some days elapsing before their normal number is restored.

Whatever future investigation may determine as to the origin of the red and white corpuscles or their relation to each other, there can be no doubt that in the adult the materials of which they are composed are derived from the food. This is well seen in the beneficial effect of giving iron in chlorosis, where the number of the red corpuscles is diminished, and which, after the use of iron, is soon restored to the normal standard. The corpuscles of the blood, however, do not exist as such in the food, but, like the other elements of the blood, must be elaborated from it.

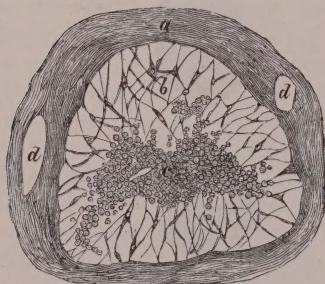
While it must be admitted that the exact manner in which the blood is elaborated is not yet understood, nevertheless the general features of the process can to a certain extent, at least, be indicated. Thus a greater part of the water found in the blood is derived from that present in the solid and liquid food, a small quantity probably being due to the combustion of hydrogen. The blood-albumen is modified albuminose, as this is modified food-albumen. The fibrin can be regarded as an effete product undergoing retrograde metamorphosis. The oleates and margarates probably result from the saponification of the fatty food by the pancreatic juice, while the iron and saline principles are evidently derived from the food.

We have seen that there are many facts which, when taken together, go to show that the red corpuscles are modified white ones. It remains for us now to consider whether any definite locality can be assigned for the production of the white corpuscles, and to ascertain, if possible, what are the elements of the food out of which they are developed.

It has already been mentioned that the white corpuscles are not confined to the blood, being also found in the lymph, chyle, etc. They are also found in the solitary and lymphatic glands, in the spleen, in the red marrow of the cancellous tissue of bones. Let us now examine the minute structure of these so-called glands and see whether the facts of comparative anatomy, pathology,

and experiment throw any light upon their relation to the white corpuscles found in them.

FIG. 108.

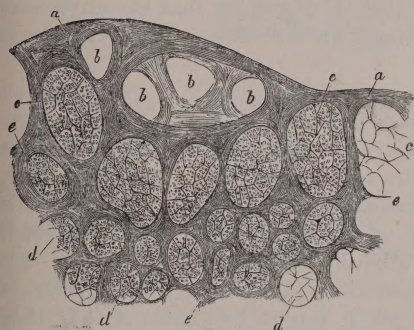


Simple lymphatic gland. *a*. The capsule with sections of lymphatics. *d*, *d*. Coursing through it. *b*. Lacunar and intercommunicating passages, permeated by the lymph, and forming the superficial lymph-path of Frey. *c*. Nucleus or medullary portion of the gland, in the centre of which the section of a bloodvessel may be seen. The path pursued by the lymph through the medullary portion constitutes the deep or secondary lymph-path of Frey. (CARPENTER.)



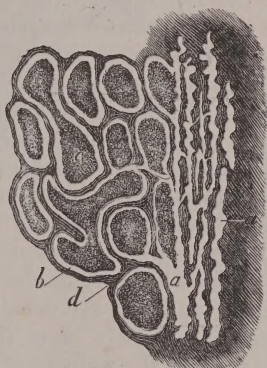
The solitary glands, as we have already noticed, are distributed all through the alimentary canal; the Peyer's patches, which consist of a number of solitary glands united together, are, however, limited to the so-called jejunum and ileum. When a section of one of these solitary or simple lymphatic glands is examined microscopically (Fig. 108) it is seen to consist of a capsule of connective tissue from which pass inwardly strands forming a meshwork, in the interior of which is contained the so-called adenoid or cytogenous tissue. These strands of connective tissue serve to support the capillary bloodvessels. In the meshes are found lymph corpuscles and sometimes molecular granules and small oil globules. Imagine a number of these solitary glands held together by a capsule of connective tissue, and we have a lymphatic gland (Fig. 109). The meshes in the lymphatic gland are, however, much closer in the centre than at the sides, hence the distinction of the medullary and cortical parts (Fig. 110). Further the meshes are only incom-

FIG. 109.



Section of lymphatic gland, showing *a, a*, the fibrous tissue which forms its exterior. *b, b*, Superficial vasa inferentia. *c, c*, Larger alveoli, near the surface. *d, d*, Smaller alveoli of the interior. *e, e*, Fibrous walls of the alveoli. (CARPENTER.)

FIG. 110.



Longitudinal section through the hilum of a mesenteric gland from the ox, showing the commencement of the efferent lymphatic vessels injected from a puncture of the glandular substance. *a*, Plexus of efferent vessels *b*, Lymph paths. *c*, Medullary cords. *d*, Trabeculae. (KÖLLIKER.)

pletely filled by the pulp, free spaces being left between the pulp and the strands. These spaces communicate on the one hand with the lymphatic vessels entering the gland, and on the other with the lymphatics leaving it at the hilus. The afferent and efferent lymphatic vessels and these spaces can be injected. Probably this is the explanation of the gland appearing after injection as a mass of vessels, a rete mirabile between and continuous with the lymphatics passing in and out of it. The pulp consists principally of lymph corpuscles, these being most numerous in the medullary parts of the gland where the bloodvessels are also freely distributed.

The lymph or chyle passes from the afferent vessels into the spaces left between the pulp and the strands, and comes in contact with the lymph corpuscles and the blood, more particularly in the medullary parts of the gland; after circulating through these spaces the lymph or chyle passes out of the gland at the hilus by the efferent lymphatic vessels, and so passes on to the thoracic duct.

8 | The researches of Klein,<sup>1</sup> von Recklinghausen,<sup>2</sup> and others, have shown that the walls of the serous sacs, like the peritoneum, pleura, etc., consist, to a considerable extent, of the adenoid or cytogenous tissue just mentioned, which enters into the formation of the solitary and lymphatic glands, and that these serous sacs communicate by openings or stomata with the lymphatics. Indeed, these sacs are now regarded as being lymphatic glands unravelled, having essentially the structure and function of the glands already described.

We have already seen that the lymph differs from the blood quantitatively, rather than qualitatively, and that the chyle is lymph with the products of digestion added to it, more especially of the emulsified fats and oils. The lymph and chyle corpuscles, which are undistinguishable from the white corpuscles of the blood, seem to consist at first of fatty nuclei, which, acquiring an envelope through diffusion in an albuminous fluid, gradually become white corpuscles. In examining the chyle of the lacteals in the villi, in the mesenteric glands, and in the thoracic duct, it was noticed that the so-called molecular base of the chyle consisted largely of fatty matter, and that the chyle corpuscles were probably due to an aggregation of the minute bodies forming the base of the chyle. It seems probable, therefore, that the chyle corpuscles, or white corpuscles of the blood, are elaborated in the lymphatic glands out of the fatty food.

In addition to containing white corpuscles, the chyle resembles an early stage of the blood in other respects, thus between the mesenteric glands and thoracic duct it will coagulate—that is, separate into clot and serum, while the chyle of the thoracic duct exhibits a reddish color, as if the white corpuscles were gradually becoming red ones. While the fats and oils are usually taken up by the lymphatics of the small intestine, we have seen that the albuminose, glucose, salts, etc., are absorbed by the radicles of the mesenteric veins. Were these substances in a proper condition for assimilation, it might be expected that they would at once pass into the general circulation. They are, however, first mixed with the blood coming from the splenic vein, and then experience still further changes as they pass through the liver on their way to the heart. Inasmuch as the lymphatic glands seem to be the organs in which the fatty portions of the food are further elaborated analogy would lead us to expect that, in certain parts of the economy, certain organs exist which effect for the albuminose substances, etc., what the lymphatic glands do for the fats.

In examining the structure of the spleen one cannot but be impressed with its great similarity to a lymphatic gland. Like the lymphatic gland, the spleen (Fig. 111) consists externally of a fibrous capsule, from which pass inward numerous strands, constituting the so-called trabeculæ, in the meshes of which is contained the splenic pulp. This consists of white blood-corpuscles, of red corpuscles in various stages of development or disintegration, of granular matter of a reddish-brown hue, blood crystals, etc. The only difference between the spleen and a

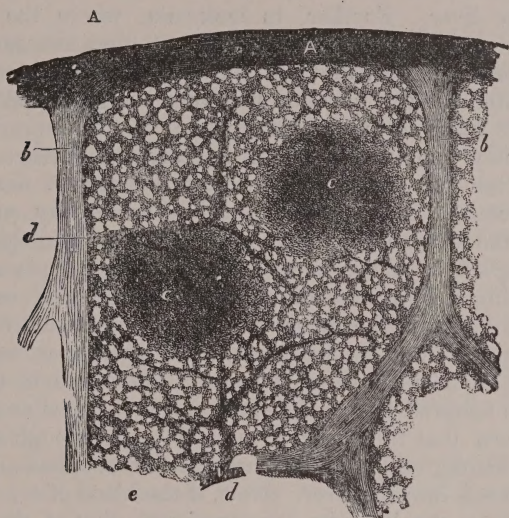
<sup>1</sup> Anatomy of the Lymphatic System, 1873.

<sup>2</sup> Stricker's Histology.



lymphatic gland consists in the fact that the cells found in the spleen pass directly into the blood.

FIG. 111.



Vertical section of a small superficial portion of the human spleen. Low power. A. Peritoneal and fibrous covering. b. Trabeculae. c, c. Malpighian corpuscles, in one of which an artery is seen cut transversely, in the other longitudinally. d. Injected arterial twigs. e. Spleen-pulp. (KÖLLIKER.)

That the spleen is structurally a lymphatic gland seems confirmed by the fact that usually when the spleen is small in man or an animal the lymphatic glands are large, and *vice versâ*. Not only is this inverse ratio observed in the same animal, but also in different species. Thus, among other instances, in the manatee (*Manatus Americanus*) the spleen is very small, while the glands are very large; while in the sea lion (*Zalophus Gillespii*) the spleen is large, and the glands are small.

One of the most striking peculiarities of the spleen is its great vascularity. Not only does a large quantity of blood flow into the organ, but in certain parts of it capillaries are absent, the blood of the splenic artery passing directly into the interstices of the splenic pulp, from which it is taken up by the veins.

It is an interesting fact that this lacunar type of circulation exhibited by the spleen is what usually obtains in the invertebrata. It may be mentioned in this connection that the so-called Malpighian corpuscles attached to the branches of the splenic artery in the spleen do not appear to differ essentially in their minute structure from that of the solitary glands. A significant fact, in connection with the development of the white corpuscles, is their great number in the blood of the splenic vein, one white corpuscle being found to every 70 red ones, whereas, in the blood of the splenic artery the proportion is only one of white to 2000 of red. The conclusion from such a contrast would not, however, be that the white corpuscles found in the splenic vein are developed in the spleen out of the red ones brought to that organ by the

splenic artery, but rather that the red blood-corpuscles are destroyed in the spleen, the disintegrated, broken-down corpuscles furnishing not only material for the development of new red blood-corpuscles, but of the coloring matter of the bile, the elaboration of the latter being effected in the liver. Further, in leukemia, where the spleen and lymphatic glands are enlarged, we have seen that the number of the white corpuscles is so great that the general color of the blood is affected by them. Naturally the question will then suggest itself as to what becomes of the white corpuscles produced in the spleen. Of what use are they if they simply disappear, and are not further elaborated? That they do not pass away is shown by their great number in the disease just referred to, in which possibly, as already suggested, the conditions or the materials for their metamorphosis into the red corpuscles are absent, such a transformation probably taking place in health.

An interesting fact in connection with the number of red corpuscles brought to the spleen is the large quantity of iron found in the splenic pulp, amounting to over seven per cent., and which may be regarded as being derived from the disintegration of the old red blood-corpuscles and serving as material for the development of the new ones.

We have seen that the portal vein is formed through the union of several veins, among others by the mesenteric and splenic, and that the portal blood passes into the liver. Now, if the blood of the hepatic vein which comes from the liver be compared with that of the portal vein which goes to the liver, it will be found that there are more corpuscles, both red and white, in the former than in the latter. It must be admitted, however, that according to some observers there are relatively fewer red corpuscles in the blood of the hepatic vein than in that of the portal. This may be due, however, to the destruction of the red corpuscles in the liver during the intervals of digestion.

The liver must, therefore, have in the adult, as in the embryo, an influence in the elaboration of the blood corpuscles. If it be admitted that the white corpuscles are produced in the spleen and are then carried by the splenic vein to the portal, where they can absorb fresh nutritive matter, albuminous substances, etc., and that they then undergo a further elaboration in the liver, becoming red ones, we have an explanation of the interesting anatomical relations of the parts just referred to. That the spleen has some such function in the process of sanguinification, as just indicated, similar to the influence exerted by the lymphatic glands upon the fatty food passing through them, is confirmed by a consideration of the absorbent system in the animal kingdom generally.

In the invertebrata and the amphioxus there is no distinction between the lymph and blood, the nutritive fluid being comparable rather to the lymph of the vertebrates than to their blood. There is also only one set of absorbents in the invertebrata. The spleen is absent in the amphioxus, while true lymphatic glands cannot be said to exist in fishes and reptiles, and are only sparingly developed in birds.

The lymphatics of the small intestine in the three latter classes are so rarely filled with chyle that, according to some anatomists, lacteals cannot be said to exist. It is only in the mammals that we find the digested food is absorbed by two distinct sets of vessels, and even in



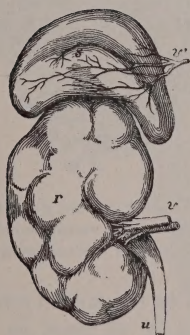
these, as we have seen, one set of vessels does at times absorb all kinds of food. In a word, both sets of vessels are combined in the lower animals, while in the higher the work of elaboration is divided between the lymphatic glands on the one hand and the spleen and the liver on the other.

Admitting that the spleen is a lymphatic gland, and that, like the latter, it elaborates white corpuscles out of fat, it may be supposed that the materials supplying the fatty principles are brought to the spleen by the splenic artery; or it may be possible that the white corpuscles developed in the mesenteric lymphatic glands having reached the spleen by the route of the thoracic duct, heart, and splenic artery, undergo there a further elaboration, finally becoming in the liver red corpuscles.

The investigations of Neuman,<sup>1</sup> Bizzozero,<sup>2</sup> and others, appear to show that lymph corpuscles are developed in the red marrow of the cancellous tissue of bones as well as in the lymphatic glands and spleen. According to Neuman, not only are both white and red corpuscles found in the red marrow but also all kinds of transitional forms between the two, nucleated granular cells of a yellowish color passing insensibly into non-nucleated cells of a reddish hue, and these gradually leading on to the red corpuscles proper.

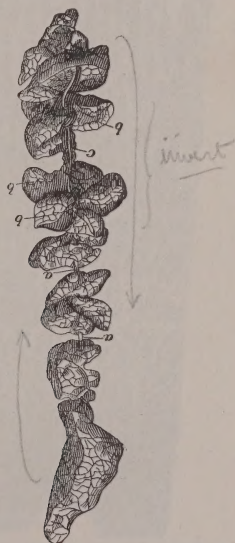
It is possible that the tonsils, the glands found in the tongue, palate, etc., may also have an influence in the production of the white corpus-

FIG. 112.



Front view of the right kidney and suprarenal body of a full-grown foetus. This figure shows the lobulated form of the foetal kidney. *r, v.* The renal vein and artery. *u.* The ureter. *s.* The suprarenal capsule, the letter is placed near the sulcus in which the large veins (*v'*) are seen emerging from the interior of the organ. (ALLEN THOMSON.)

FIG. 113.



Portion of thymus of calf, unfolded. *a.* Main canal. *b.* Glandular lobules. *c.* Isolated gland-granules seated on the main canal. (CARPENTER.)

cles. From this general survey it will be seen that probably the white corpuscles are produced in several parts of the economy, and that a kind

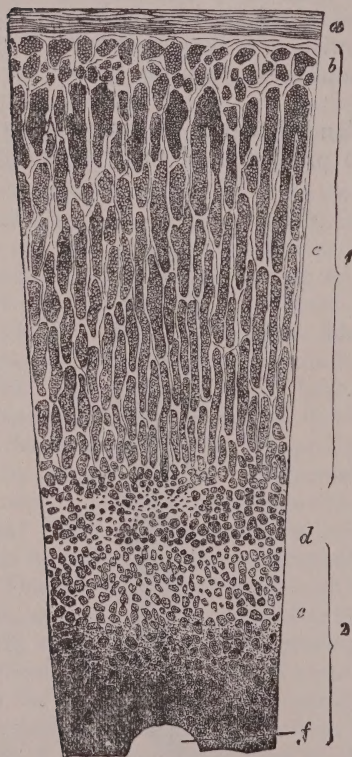
<sup>1</sup> Archiv der Heilkunde, 1869.

<sup>2</sup> Centralblatt, 1868.

of vicarious action may take place among the organs concerned in their production. Thus, if the spleen be extirpated, the lymphatic glands become enlarged and more active. With hypertrophy of spleen we have, coincidentally, disease of the bones, which becomes intelligible when it is remembered what has just been said with reference to the marrow and the blood corpuscles, and that the function of the spleen is of such a supplementary character to that of the lymphatics as already described is still further shown from the fact that it can be entirely removed from the body of an animal without the functions of the latter being apparently in any way interfered with, the lymphatic glands then enlarging proportionally to the greater amount of work thrown upon them.

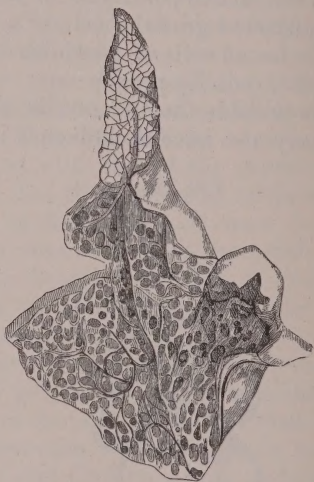
The suprarenal capsules, Fig. 112, and thymus glands, Fig. 113, are at the present day considered by many physiologists as having the same

FIG. 114.



Vertical section of suprarenal capsule of man. 1. Cortex. 2. Medulla. *a.* Capsule. *b.* Layer of external cell-masses. *c.* Columnar layer (zona fasciculata). *d.* Layer of the internal cell-masses. *e.* Medullary substance. *f.* Section of a vein. (CARPENTER.)

FIG. 115.



Section of human thymus, showing a cavity in the wide portion, and numerous orifices leading to its lobular cavities. (CARPENTER.)

function as the spleen and lymphatic glands, at least in the embryo if not in the adult. The structure of the suprarenal capsules (Fig. 114) recalls that of a lymphatic gland, consisting, as it does to a great extent, of trabeculae, in the ovoid meshes of which are imbedded nuclear capsules, cells with granular contents, with and without nuclei, of oil and pigmentary matter, yet it must be admitted that their functions are still very obscure.

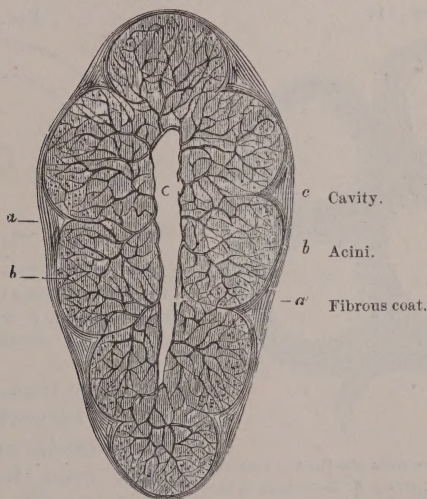


From the fact <sup>that</sup> the suprarenal capsules being relatively most developed in the embryo, their function, whatever it may be, is possibly restricted to foetal life.

The immense number of nerves distributed to these bodies is one of their most remarkable peculiarities, the significance of which is, however, unknown. The bronzing of the skin often associated with disease of the suprarenal capsules, does not as yet throw light upon the functions of these bodies, inasmuch as the bronzing may be present without disease of the suprarenal capsules, and these bodies may be diseased and yet the skin unaffected.

It is generally stated that the thymus gland is also restricted in its functions to foetal life. According to Carpenter,<sup>1</sup> however, it is soon after birth that the gland is most active, and that even till the age of puberty it continues to increase in size. The thymus gland appears in the embryo first as a solid body, but soon becomes a tube closed at both ends and filled with granular matter. From this tube (Fig. 115) there bud out at intervals, on either side, hollow lobular processes, the cavities of which communicate with that of the central axis. The thymus in the adult consists of a series of such offshoots or lobules united by connective tissue and opening into the central tube, to which, however, there is no outlet. Each lobule (Fig. 116) consists of an external

FIG. 116.



Section of lobule of thymus.

fibrous capsule which sends prolongations into its interior consisting of acini, in the meshes of which are seen the thymus substance. This contains lymph corpuscles, spheroidal granular bodies, and concentric corpuscles. In the expressed thymus juice are found corpuscles which are undistinguishable from those of the fluids of the lymphatic glands. The thymus gland, in its whole structure, is very much like a Peyer's

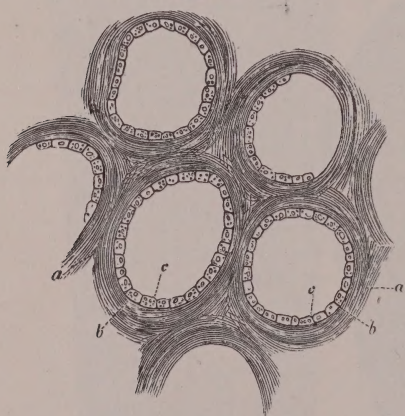
<sup>1</sup> Physiology, p. 216.

patch. The fact of the thymus being most active during foetal life, and for some time after birth, makes it probable that it, and possibly the suprarenal capsules, influences the elaboration of blood in the embryo in the same manner as the spleen and the lymphatic glands do in the adult.

The thyroid gland, like the thymus, relatively larger in the foetus and in the infant than the adult, is also regarded at present by many physiologists as having an influence in sanguinification. Its remarkably rich vascular supply would lead one to consider it as performing some function in the elaboration of the blood, either as eliminating some effete material from the blood or furnishing it with nutritive material. As there is no excretory duct to the thyroid gland, the latter view of its function is the more probable. The development of a goitre or enlargement of the thyroid gland, may be possibly due to the retention of matters by the gland which are ordinarily given up to the blood circulating through it, while the want of such material in the blood circulating through the brain may be connected with the idiocy so often associated with goitre. In the same way the white appearance of young women affected with tumors of the thyroid gland may be due to the retention by the gland of material which it usually furnishes to the blood supplying it.

The structure of the thyroid gland differs from the spleen or lymphatic glands, it consisting of a collection of vesicles (Fig. 117) imbedded in

FIG. 117.



Group of gland-vesicles from the thyroid gland of a child. *a* Connective tissue. *b* Membrane of the vesicles. *c* Epithelial cells. (CARPENTER.)

FIG. 118.

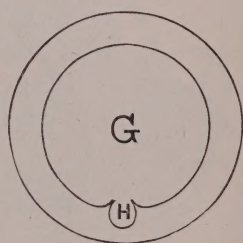


Diagram illustrating the relation of the respiratory chamber, G, to the hypobranchial groove, H, in ascidians. (GEGENBAUR.)

connective tissue, which also supports a network of lymphatics. These vesicles are lined with epithelial cells, from which there exudes an albuminous granular material. According to Wilhelm

Muller,<sup>1</sup> however, the thyroid gland in man is to be viewed as the rudiment of the hypobranchial groove of the ascidians and the amphioxus, which, traversing the middle of the gill body (Fig. 118) of these animals, assists in conducting the food into the stomach. When all the facts are considered together, the following general conclusion may be drawn: that the spleen, the lymphatic and solitary glands, the

<sup>1</sup> *Jenaische Zeitschrift*, 1873, Band viii. S. 327.



Peyer's patches, have essentially the same structure and perform the same functions, that of producing the lymph-or white-corpuses; that probably the thymus, and possibly the suprarenal capsules, has the same function, but restricted in its performance to the early periods of life; that the thyroid, while differing from the glands just mentioned in its minute structure, yet has some influence in the process of sanguification; that the red corpuscles are developed from the white, the elaboration taking place in different parts of the economy—the red marrow and the liver, for example—and that, having played their part, they pass away like all other organites.

The blood contains, in addition to the red and white corpuscles, minute granules or molecules. These are of a circular form, attaining sometimes the size of the  $\frac{1}{8000}$ th of an inch, but are usually much smaller. They resemble the minute fatty particles of which the molecular base of the chyle consists. Some of them are, however, of an albuminous nature. It is possible that these elementary corpuscles, as they have been called, are undeveloped lymph-or white-corpuses.

## CHAPTER XV.

### THE BLOOD.—(*Continued.*)

ONE of the most interesting facts about blood is its power of coagulation, or of its separation into clot and serum. Before coagulation the blood consists of the liquor sanguinis or plasma and the corpuscles; after coagulation it will be found that the corpuscles are entangled in the meshes of the coagulated fibrin, the two constituting the clot or crassamentum, while the albumen, salts, and water remain together as the serum. It is important to notice that the liquor sanguinis, or the plasma, is not identical with the serum. As may be seen from Table XLII., the liquor sanguinis is serum with the addition of fibrin, and that serum is liquor sanguinis without fibrin. Serum differs also from what are known as serous effusions, which are due to transudations, not to coagulation.

TABLE XLII.—BLOOD.

| Before coagulation. |   |         |   |   |   |   |   |   |   | After coagulation. |  |
|---------------------|---|---------|---|---|---|---|---|---|---|--------------------|--|
| Liquor sanguinis    | { | Water   | . | . | . | . | . | . | } | Serum.             |  |
|                     |   | Salts   | . | . | . | . | . | . |   |                    |  |
|                     |   | Albumen | . | . | . | . | . | . |   |                    |  |
|                     |   | Fibrin  | . | . | . | . | . | . |   |                    |  |
| Corpuscles          | . | .       | . | . | . | . | . | . | . | Clot.              |  |

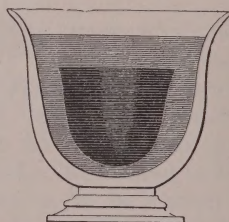
When the blood is allowed to flow into a tolerably deep, smooth vessel, according to Nasse,<sup>1</sup> in from about one minute and forty-five seconds to six minutes a gelatinous layer will be seen to form on its surface, in from two to seven minutes the sides of the vessel are covered with a similar layer, and in from seven to sixteen minutes the whole

FIG. 119.



Bowl of recently coagulated blood, showing the whole mass uniformly solidified. (DALTON.)

FIG. 120.



Bowl of coagulated blood, after twelve hours; showing the clot contracted and floating in the fluid serum. (DALTON.)

of the blood becomes jelly-like (Fig. 119); gradually there exudes from the contracting jelly-like mass, drop by drop, a fluid, the serum, and in

<sup>1</sup> Wagner: Physiologie, 1842, Band 1, S. 104.



from ten to twelve hours the coagulation is complete—that is, the separation of the blood into clot and serum (Fig. 120.) The contracted jelly-like red mass, the clot, being heavier (specific gravity of corpuscles, 1.088), usually falls to the bottom of the straw-colored or reddish liquid, the serum (specific gravity, 1.028), surrounding it, which has exuded from it.

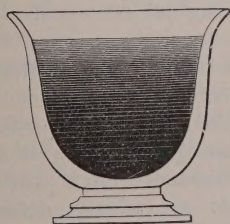
Usually, according to Milne Edwards,<sup>1</sup> the clot retains about one-fifth of the entire volume of the serum; this should be remembered when the proportion of clot to serum is estimated; it is generally stated that they are equal. When the coagulation has been slow, the clot will be found to be firm; on the other hand, when the coagulation has been rapid, the clot is soft. When blood coagulates slowly, and so remains fluid for some time, the red corpuscles, on account of their weight, sink and settle at the bottom of the clot; the upper part of the clot will be, therefore, much lighter in color than the lower, and, when white, is known as the buffy coat (Fig. 121); it is almost always seen in the blood of the horse, which coagulates slowly (Table XLIII.), while it is absent in the pigeon, in which the blood coagulates almost instantaneously.

TABLE XLIII.<sup>2</sup>—LENGTH OF TIME OF COAGULATION.

| Animal.         | Minutes.                        | Animal.          | Minutes.                        |
|-----------------|---------------------------------|------------------|---------------------------------|
| Man . . . . .   | 2 to 16                         | Rabbit . . . . . | $\frac{1}{2}$ to $1\frac{1}{2}$ |
| Horse . . . . . | 5 to 13                         | Lamb . . . . .   | $\frac{1}{2}$ to 1              |
| Ox . . . . .    | 2 to 12                         | Duck . . . . .   | $\frac{1}{2}$ to 2              |
| Dog . . . . .   | $\frac{1}{2}$ to 3              | Fowl . . . . .   | $\frac{1}{2}$ to $1\frac{1}{2}$ |
| Sheep . . . . . | $\frac{1}{2}$ to $1\frac{1}{2}$ | Pigeon . . . . . | almost instantaneously.         |
| Hog . . . . .   | $\frac{1}{2}$ to $1\frac{1}{2}$ |                  |                                 |

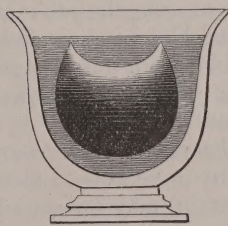
When contraction of the clot takes place most rapidly at the edges, these curl up and the upper surface becomes concave or cupped (Fig. 122). For many years it was supposed that the buffy coat was char-

FIG. 121.



Vertical section of a recent coagulum, showing the greater accumulation of blood globules at the bottom. (DALTON.)

FIG. 122.



Bowl of coagulated blood, showing the clot buffed and cupped.

acteristic of inflammation, whereas it is now known that the buffy coat is also present in diseases of a totally opposite character—in chlorosis, for example, it depending here upon a diminution of the blood-corpuscles. It is obvious that bleeding in such cases would only

<sup>1</sup> Physiologie, tome i. p. 124.

<sup>2</sup> Thakrah : Inquiry into the Nature of Blood, 1819, p. 29.

increase the buffy coat by diminishing still further the corpuscles, and yet, when it is remembered that bleeding was once the sovereign remedy for inflammation, one can readily imagine the number of lives that must have been sacrificed through the mistaken idea of the buffy coat being always due to inflammation.

We shall see that the fibrin is increased in inflammation, and in inflammation the blood also coagulates slowly; the appearance of the buffy coat under such circumstances, therefore, is perfectly intelligible. It must not be forgotten that the formation of the buffy coat is simply a question of time, as shown by the researches of Polli,<sup>1</sup> for as coagulation is either retarded or accelerated, so will the buffy coat be formed or not formed.

There is no better illustration of the great influence that the progress of physiology exerts upon the practice of medicine, than the history of the blood. Dr. Carpenter,<sup>2</sup> in his most thoughtful work, in speaking of this subject, well says: "If Andral had made no other contribution to medical science than the demonstration of the real nature of this condition of the blood, and of further depletion in promoting it, he would have rendered a most essential service to the multitude of females who are unfortunate enough to suffer from this kind of deterioration of their vital fluid."

It is well known that there are various circumstances which modify the coagulation of the blood. Thus, blood flowing from a small orifice coagulates more quickly than when flowing from a large one, and more quickly when it is received in a shallow rough vessel than when in a deep smooth one. Blood coagulates more rapidly in a vacuum than in the air. Rapid freezing prevents the coagulation of the blood; this will take place, however, after careful thawing. This fact is of importance from a medico-legal point of view.

Elevation of temperature between 32° and 140° Fahr. increases the rapidity of coagulation. Chemical substances, like solutions of soda and potash, ammonium and sodium sulphate and carbonate, will retard or prevent coagulation. It is due to the vaginal secretions that the menstrual blood is kept fluid.

The blood not only coagulates outside the body, but also after death within it; less rapidly, however, and, as a rule, in from twelve to twenty-four hours after death. It is not unusual, also, during life to find clots in the heart and other parts of the vascular system. As it is often important to be able to distinguish an ante-mortem from a post-mortem heart-clot, it may be stated that the former are whiter, denser, and adhere more closely to the walls of the heart than the latter. Coagula are also found when an artery is ligated, in the enlarged veins of hemorrhoids, in the varicose veins of the extremities. Usually the blood coagulates when effused into the areolar tissue or the cavities of the body. It is an interesting fact, however, that the blood may remain fluid in the serous cavities for days and weeks at a time. When coagula are formed in the heart, and being swept into the circulation are carried thence into the small vessels of the brain, etc., they consti-

<sup>1</sup> *Annali universali di medicina*, 1843.

<sup>2</sup> *Physiology*, p. 267.



tute what are known as emboli. When the blood coagulates in the economy it acts as a foreign body, but is usually absorbed, though this may take a long time. The corpuscles first disappear, then the fibrin softens, breaks down, and is finally carried away.

The coagulability of the blood is nature's cure for hemorrhage, and when this power is diminished or wanting we have the hemorrhagic diathesis, where the slightest wounds are followed by severe, and sometimes fatal hemorrhage. As the above facts belong rather to the province of pathology I merely mention them here in an incidental way.

From time immemorial various explanations have been offered of the coagulation of the blood. A favorite one has been that of the blood being maintained in the body in a liquid condition through the influence of life. Apart from this being no explanation at all, but simply a statement of the phenomena to be explained, it is not even a fact, as we have seen that the blood coagulates in the living body. In the last century it was generally held that what we call fibrin was produced in some way at the expense of the corpuscles, which run together in coagulation, etc. Petit, Davies, and Hewson,<sup>1</sup> however, held that coagulation was due to some substance separate from either the corpuscles or the serum, and Hewson performed several experiments to prove that coagulation was due to the fibrin. For example, Hewson<sup>2</sup> added a little sodium sulphate to fresh blood, which prevented coagulation. After the mixture had remained standing some time the corpuscles sank to the bottom, the clear fluid which remained on top was then decanted, twice its quantity of water was then added to this, when the fibrin coagulated. On another occasion, this most able observer<sup>3</sup> tied the jugular veins at the sternum of a dog just dead, and hung his head over the edge of a table, so the ligatures might be highest, the upper part of the vein became transparent, the red corpuscles sinking; he then tied the vein, separating the clear from the muscular part, and let the clear part out, which was fluid, but coagulated soon after. These experiments showed that the coagulation was due to the fibrin, but they did not demonstrate that this fibrin did not come from the corpuscles, which was the view that prevailed at that time. To do this it was necessary to show that the corpuscles were unaffected to coagulation.

With reference to determining this point, Johannes Muller,<sup>4</sup> the great Berlin physiologist, in 1832 experimented in the following ways: He added a little solution of sugar to frog's blood, which retarded the coagulation, and then filtered the mixture; the corpuscles, which are very large, were retained in the filter, and the clear fluid which passed through coagulated. Muller then showed that in blood which was defibrinated by whipping, and therefore incoagulable, ~~that~~ the corpuscles were not altered in any appreciable manner; and further, that when blood to which had been added serum (which separated the corpuscles from each other) was observed under the microscope coagulating, the corpuscles were seen to remain intact.

Inasmuch as the white stringy substance appearing at the moment

<sup>1</sup> Milne Edwards, *op. cit.*, tome i. p. 119.

<sup>4</sup> *Physiology*, transl. by Baly, 1840, vol. i. p. 123.

<sup>2</sup> *Works*, p. 12.

<sup>3</sup> *Ibid.*, p. 32.

of coagulation, which we call fibrin, evidently does not exist as such in the blood before coagulation, it remains to be determined, if possible, under what form it then does exist. If blood be drawn into a concentrated solution of sodium sulphate to prevent its coagulation, and sodium chloride be added to the mixture in the proportion of ten per cent., a whitish, pasty substance is thrown down, amounting to about 25 parts per 1000 of the blood used, and called by Denis,<sup>1</sup> who first described it, plasmin, and which, together with serin, constitutes blood albumen. Now, when plasmin is redissolved in water, the solution splits into fibrin 3 parts, and paraglobulin 22 parts, the former coagulating, the latter remaining liquid. It would appear, therefore, that fibrin exists in the blood combined with paraglobulin, as plasmin or some form closely allied to it; and further, as with the withdrawal of the plasmin from the blood, the latter loses its power of coagulating, the serin remaining liquid, that coagulation of the blood consists, first, in the splitting of albumen into serin and plasmin, and secondly, in the latter splitting into fibrin and paraglobulin, or of the breaking up of albumen directly into serin, fibrin, and paraglobulin.

On the other hand, the observation, made many years ago by Buchanan,<sup>2</sup> that two fluids, like that of hydrocele and ascites, for example, or of ascites and pleurisy, when added together, coagulate, though when separate show no such tendency, has led many to infer that the production of fibrin is rather due to the union of substances in the blood than to the decomposition of the same, as just explained. Indeed, according to Schmidt,<sup>3</sup> two such principles actually do exist in the blood, a fibrinoplastic substance, paraglobulin, and a fibrinogenous one, fibrinogen, whose union brought about by the presence of a ferment at the moment of coagulation constitutes fibrin.

Paraglobulin can be readily obtained from the serum of the blood through precipitation by the addition of sodium chloride in excess, and fibrinogen in the same way free from the liquor sanguinis, in which coagulation has been prevented by the addition of magnesium sulphate, and the corpuscles have been removed by filtration.

Now, while it is an interesting fact that if paraglobulin in a saline solution be added to either fibrinogen or hydrocele fluid, or if fibrinogen as obtained either from the liquor sanguinis or hydrocele fluid be added in saline solution to serum, fibrin will be produced, it does not necessarily follow that such a union as that of paraglobulin and fibrinogen actually takes place in the blood at the moment of coagulation. Indeed, it is yet to be proved that paraglobulin exists as such in the clot, seeing that if we obtain it from the serum it must be assumed that it exists in excess partly in the serum and partly in the clot. Again, as under certain circumstances, paraglobulin when mixed with fibrinogen does not produce fibrin, it is still further assumed that the presence of a ferment is necessary to effect the union of the two fibrin factors. As a matter of fact, an aqueous extract can be obtained from the serum by coagulating the latter with alcohol, allowing the mixture to stand,

<sup>1</sup> *Annales des Sciences Naturelles* (iv.), p. 25.

<sup>2</sup> *Proc. of Glasgow Philos. Soc.*, 1845.

<sup>3</sup> Du Bois Reymond: *Archiv*, 1861, S. 545; 1862, S. 428. Pflüger's *Archiv*, 1872, S. 413; 1875, S. 291; 1876, S. 515.



drying and pulverizing the clot, and then adding water and filtering, which, when added to fibrinogen will cause the coagulation of the latter like a ferment. According to Schmidt, such a ferment is derived from the disintegration of the white corpuscles, the latter, as is well known, being always present in spontaneously coagulable fluids and very abundant if the coagulation is marked.

It remains to be shown, however, that this ferment is actually present at the moment of coagulation and exercises then the influence attributed to it of effecting the union of the fibrin factors, supposing such to exist in the blood. It is far therefore from being proved, as is often assumed, that the formation of fibrin is due to the union of paraglobulin and fibrinogen through the influence of a ferment. Indeed, according to some experimenters, Fredericq,<sup>1</sup> Hammersten<sup>2</sup>, the clot is due to the coagulation of the fibrinogen alone through the influence of a ferment; the paraglobulin, however, not entering into the formation of the clot at all, the amount of the clot depending only on that of the fibrinogen present.

The fibrin factor theory offered of coagulation is based rather upon assumptions and inferences than upon demonstrations. There appears to be a tendency at present<sup>3</sup> also to return to the view of the older physiologists, already referred to, that the red corpuscles contribute to the formation of the clot in coagulation, since if these elements are separated by decantation from a given quantity of blood and added to an equal amount of serum the latter will coagulate, while the quantity of fibrin produced bears a very considerable proportion to the whole quantity which the blood would have yielded.

It is difficult to see how the corpuscles can contribute to the formation of the clot, supposing this to consist of paraglobulin and fibrinogen, since the former is obtained from either the serum or the plasma and the latter from the liquor sanguinis. Further, the lymph coagulates even in the absence of red corpuscles. In truth it must be admitted that, whether we suppose with Denis that coagulation is due to the decomposition of certain principles in the blood, or with Schmidt to the union of others, the cause of the phenomena is as obscure as the assumption that fibrin exists in a liquid condition in the blood and coagulates through some unknown influence, as albumen does by heat.

<sup>1</sup> Hoppe-Seyler : *Physiologie Chemie*, 1879, S. 416.

<sup>3</sup> Sanderson : *Handbook*, 1873, p. 182.

<sup>2</sup> Pflüger's *Archiv*, Band xix. S. 563.

## CHAPTER XVI.

### COMPOSITION OF THE BLOOD.

WE have seen that the blood contains, either directly or indirectly, all the proximate principles of which the body is composed, including also the excrementitious matters, and that the food furnishes the materials out of which the vital fluid is elaborated.

As the composition of the blood must therefore vary in different individuals, and even in the same person from day to day and from hour to hour, anything more than an approximate analysis cannot be expected. The discrepancies as offered by the analyses of different chemists are due not only to this cause, but to the various methods made use of by them.

As the object of an analysis of the blood from a physiological point of view is to show not only the ultimate chemical elements entering into its composition, but the manner in which these exist in the blood, it will be readily understood that the investigation is an extremely difficult one.

While it is not necessary to describe in detail the analyses of the blood that have been made by different chemists, it seems proper that, at least, attention should be called to the general methods of investigation made use of at the present day.

During the last and preceding century a number of observations were made by which it was shown that the blood consisted of different principles. Thus Harvey discovered the albumen, Malpighi and Ruysch the fibrin, Guglielmini and Menghini some of the salts, Badia the iron, Rouelle the soda, etc.

Passing over these early and isolated observations,<sup>1</sup> it may be said that Macquer, a little more than a century ago, made the first analysis of the blood as a whole. With improved methods of chemical investigation the blood was more successfully analyzed by Berzelius in 1808. Some years later, 1823, Prevost and Dumas<sup>2</sup> published the results of their elaborate researches upon the constitution of the blood, and as their investigations have served as the starting-point for later analyses let us briefly review the method employed by these eminent chemists.

The blood to be analyzed is received into two equal vases, that of one vase is whipped so as to obtain the fibrin, which when entirely separated is weighed. The blood in the other vase is set aside to coagulate—that is, to separate into clot (fibrin and corpuscles) and serum (albumen, salts, water). The clot and serum are then separated and desiccated so as to obtain the amount of water in them, and therefore in the blood of the second vase. As the clot consists of fibrin and corpuscles, if we subtract from the clot the fibrin obtained from the blood of the first vase, the remainder will give the quantity of the corpuscles in the

<sup>1</sup> Milne Edwards : *Physiologie*, tome i. p. 141.

<sup>2</sup> *Ann. de Chimie et de Physique*, 1823, tome xxiii. p. 50.



blood of the second vase, or one-half the quantity in the whole blood examined. Having determined then the fibrin, water, and corpuscles, there remains the desiccated serum of the second vase to be analyzed for the albumen and the salts; the latter are determined by ordinary chemical analysis. Becquerel and Rodier determined the amount of albumen by treating the desiccated serum with boiling water, which separates the undetermined extractive matters and soluble salts, and then with alcohol, which dissolves the fats, the remainder being the albumen.<sup>1</sup> Figuier<sup>2</sup> suggested the improvement of estimating the corpuscles by adding to the defibrinated blood twice its volume of a solution of sodium sulphate and then filtering, the corpuscles can be counted, the saline retaining them on the filter; any sodium sulphate that remains on the filter can be removed by boiling water. Figuier's method of estimating the corpuscles can also be used as confirmatory of that of Dumas. The quantity of the corpuscles is estimated in their dry condition.

TABLE XLIV.—COMPOSITION OF THE BLOOD.

|                                                                     |                 |
|---------------------------------------------------------------------|-----------------|
| Water . . . . .                                                     | 781.600         |
| Globules . . . . .                                                  | 135.000         |
| Albumen . . . . .                                                   | 70.000          |
| Fibrin . . . . .                                                    | 2.500           |
| Serolin . . . . .                                                   | 0.025           |
| Cholesterin . . . . .                                               | 0.125           |
| Sodium { Oleate<br>Margarate<br>Stearate } . . . . .                | 1.400           |
| Potassium { Chloride . . . . .                                      | 3.500           |
| Sodium {<br>Magnesium {                                             |                 |
| Sodium { Carbonate<br>Potassium { Sulphate<br>Phosphate } . . . . . | 2.850           |
| Free Soda { Sulphate<br>Magnesium { Phosphate } . . . . .           |                 |
| Calcium phosphate . . . . .                                         |                 |
| Iron . . . . .                                                      | 0.550           |
| Extractives undetermined . . . . .                                  | 2.450           |
|                                                                     | <hr/> 1.000.000 |

The general results of an analysis of the blood by such a method as that just given may be seen from Table XLIV., taken from Becquerel and Rodier's work, and which undoubtedly gives a very fair idea of the average composition of the blood from a purely chemical, and, indeed, to a certain extent, from a physiological point of view also. It will be noticed at once, however, that in this analysis of a 1000 parts of blood, there are present only 135 parts of corpuscles; whereas, anyone who is familiar with the appearance of living blood under the microscope knows that the corpuscles bear a much larger proportion, forming, perhaps, half of the mass of blood examined. This discrepancy is perfectly accounted for when we remember that, by the method of Becquerel and Rodier, the clot from which the corpuscles are estimated is dried and

<sup>1</sup> Traité de chimie de pathologique, p. 20. Paris, 1854.

<sup>2</sup> Ann. de Chimie, et de Phys., 1844, 3me serie, tome xi. p. 506.

their water therefore driven off; the 135 parts of corpuscles represent, therefore, dry ones and not the living corpuscles, which, when united with their 370 parts of water, will amount to nearly 500 parts in the 1000 of blood analyzed.

Judging, also, from the boiled serum, we should expect to find a greater quantity of albumen than 70 parts per 1000 of blood. In the analysis just given the serum from which the albumen is determined is dried like the clot, hence the water present in living albumen is not given. When the water, however, is taken into consideration, the albumen will then amount to more than 300 parts in 1000 of blood. As the object of the physiologist is to ascertain if possible the quantity of albumen, fibrin, and corpuscles, as they exist in living blood, and as in this condition water is an indispensable element of their composition, it becomes a matter of importance to determine the quantity of these principles in a moist as well as in the dry condition. For these reasons Prof. Flint, in his excellent work,<sup>1</sup> suggests that, while the fibrin be obtained in the usual manner of whipping—with broom-corn, for example—and the corpuscles by Figuier's filtering method, both these principles should be estimated in their moist condition, and not after desiccation; and that in determining the albumen from the serum, this should be treated as described above, but in the condition that it is found after coagulation—that is, with its water.

The difference between the results of an analysis of the blood by the method of Prof. Flint and that of MM. Becquerel and Rodier, may be seen from Table XLV. The excess of water in the analysis of the latter is distributed between the albumen, fibrin, and corpuscles in that of the former.

TABLE XLV.—COMPOSITION OF THE BLOOD

(as analyzed by the methods of Flint, and Becquerel and Rodier).<sup>2</sup>

|                                | Flint.   | Becquerel and Rodier. | Difference is in water. |
|--------------------------------|----------|-----------------------|-------------------------|
| Water . . . . .                | 154.870  | 790.070               | 635.200                 |
| Albumen . . . . .              | 329.820  | 71.530                | 258.290                 |
| Fibrin . . . . .               | 8.820    | 2.500                 | 6.320                   |
| Corpuscles . . . . .           | 495.590  | 125.000               | 370.590                 |
| Remaining matters, salts, etc. | 10.900   | 10.900                | 00.000                  |
|                                | 1000.000 | 1000.000              |                         |

We say the method of Becquerel and Rodier, not their actual analysis, for the quantities of albumen, fibrin, and corpuscles given under the methods of Becquerel and Rodier in Table XLV., were experimentally obtained by Prof. Flint by weighing the dry residue after desiccating these principles obtained by his method. It is very satisfactory, however, to see that the difference between the quantities of dry albumen and corpuscles given by Prof. Flint (Table XLV.) and Becquerel and Rodier (Table XLV.) are very slight, and that the quantity of fibrin is the same according to both. The remaining matters of the blood are determined in the same manner by these and other authorities by the ordinary methods of chemical analysis.

<sup>1</sup> Physiology, vol. ii. p. 133.

<sup>2</sup> Becquerel and Rodier, op. cit., 86.



Of these, the larger proportion are the inorganic principles, and from <sup>these</sup> a purely chemical point of view, have been very satisfactorily determined, <sup>these</sup> both quantitatively and qualitatively; but of the exact manner in which they exist in the living blood little is known beyond a few general statements to be noticed shortly.

The analyses of Prevost and Dumas, Andral and Gavarret, Lehmann, Becquerel and Rodier, Simon, Denis, Gorup Besanez, etc., while differing in detail, agree substantially in showing that the blood consists of water in molecular combination with or holding in solution albuminous substances, fats and sugars, and saline matters. It is interesting to observe in this connection that milk and eggs, the food of the young animal and embryo, consist of a mixture of water, albumen, fats, sugars, and salines, approximating closely in their composition to that of the blood; the value of such articles of food at all stages of life will be therefore readily understood.

We have seen that, under natural circumstances, the diet of man is a mixed one, and that beyond a limited period of time no single article of food, solid or liquid, will sustain life. As the blood is elaborated from the food it becomes impossible, therefore, to say positively that any one of its constituents is more indispensable to life than another. It is immaterial, therefore, with which I commence in describing their quantitative relations. I will follow, then, the order in which they present themselves in the analysis given by Becquerel and Rodier (Table XLIV.).

The absolute amount of water found in the blood, according to this analysis, amounts to 781.600 parts in the 1000; of this we have seen in life that over 600 parts enter into molecular combination with the albumen, fibrin, and corpuscles, forming an integral part of their composition. As the great use of water to the system has already been pointed out, it will not be necessary to dwell further on the importance of the large proportion in which it is present in the blood, merely stating that while the quantity varies within slight limits, any excess that may be taken in as food is rapidly eliminated by the skin, kidneys, etc., and that a deficiency in any amount materially alters the character of the blood.

Although water forms three-fourths of the blood, and however indispensable it may be to health, yet the researches of Prevost and Dumas showed long since that there exists an intimate relation between the richness of the blood in organic matters and the vital activity of the organism.

A glance at Table XLVI. shows that the quantity of water is large in all vertebrates, but that there is more water in the blood of the comparatively inactive fishes and batrachia than in birds and mammals, and that in those mammals which hibernate, implying a low order of vitality, the blood contains more water than in the ordinary members of this class. As regards the quantity of solid matters contained in the blood of vertebrates, the birds, whose vital activity is very high, come first, the mammals next, and finally the cold-blooded batrachia and fishes. Although in Table XLVI. the fibrin and corpuscles are estimated together, we shall see in a moment, from numerous facts, that this vital power

depends upon the corpuscles especially, which vary in quantity under different conditions, whereas the proportion of fibrin and albumen is not so materially changed.

TABLE XLVI.<sup>1</sup>—PROPORTION OF WATER, ETC., IN 1000 PARTS OF BLOOD OF VERTEBRATES.

| Animal.              | Water. | Clot. | Albumen and salts. |
|----------------------|--------|-------|--------------------|
| Chicken . . . . .    | 780    | 157   | 63                 |
| Pigeon . . . . .     | 797    | 156   | 47                 |
| Duck . . . . .       | 765    | 150   | 85                 |
| Raven . . . . .      | 797    | 146   | 56                 |
| Heron . . . . .      | 308    | 132   | 59                 |
| Monkey . . . . .     | 776    | 146   | 78                 |
| Man . . . . .        | 784    | 129   | 87                 |
| Guinea-pig . . . . . | 785    | 128   | 87                 |
| Dog . . . . .        | 812    | 124   | 65                 |
| Cat . . . . .        | 795    | 102   | 84                 |
| Goat . . . . .       | 814    | 103   | 83                 |
| Calf . . . . .       | 826    | 91    | 83                 |
| Rabbit . . . . .     | 838    | 94    | 68                 |
| Horse . . . . .      | 818    | 92    | 89                 |
| Sheep . . . . .      | 836    | 86    | 77                 |
| Eel . . . . .        | 846    | 94    | 60                 |
| Frog . . . . .       | 884    | 69    | 46                 |
| Trout . . . . .      | 864    | 64    | 72                 |
| Lotte . . . . .      | 886    | 48    | 66                 |

Milne Edwards, in his elaborate work,<sup>2</sup> cites as examples the following facts. The number of corpuscles is greater in man than in woman, in the adult than in youth or in old age, in the sanguineous than in the lymphatic temperament, in pregnant than in non-pregnant women, in plethoric than in anæmic persons, or in those who have lost blood or have been without food. According to Bakewell,<sup>3</sup> the number of corpuscles differs in the blood of the Mohamedan, Hindoo, and Negro races so much so that their blood can be distinguished by this characteristic.

In all these instances where the corpuscles are in excess the vital activity is high. This statement holds good when classes of animals are compared, as may be seen from Table XLVI. by estimating separately the corpuscles and fibrin which constitute the clot, and when particular animals in a class are considered. Thus in the hibernating mammals, which sleep for months at a time, the number of corpuscles is less than in the more active ones. The blood of the pig, whose nutrition is most active, contains more corpuscles than that of any other mammal. Numerous other examples might be offered, but the above will suffice to illustrate the view that the normal amount of the blood corpuscles is the most important condition in maintaining the force of the constitution, and that any deficiency entails feebleness. This, indeed, was the opinion held more than a century ago by that most profound of physiologists, John Hunter.

Let us now consider the composition of the corpuscles. We shall see in a moment that when the blood is first cooled and then heated the

<sup>1</sup> Ann. de Phys. et de Chimie, 1823, 1re serie, t. xxiii. p. 64.

<sup>2</sup> Op. cit., tome i. pp. 231-254.

<sup>3</sup> Med. Times and Gazette, p. 514. London, Nov. 1872.



material of which the corpuscles are composed separates into two substances, the colorless stroma or globulin, and the coloring matter, the hæmoglobin or the hæmatocrystallin, which when further modified becomes hæmatin. As these two substances are albuminous in nature, it may be said that they represent in the corpuscles (Table XLVII.) the albumen and fibrin of the liquor sanguinis.

TABLE XLVII.<sup>1</sup>—BLOOD, IN 1000 PARTS EACH.

|                               | Corpuscles, 513. | Liquor sanguinis, 487. |
|-------------------------------|------------------|------------------------|
| Density . . . . .             | 1.0885           | 1.028                  |
| Water . . . . .               | 681.63           | 901.51                 |
| Solid matters . . . . .       | 318.37           | 98.49                  |
|                               | <hr/> 1000.00    | <hr/> 1000.00          |
| Hæmatin . . . . .             | 15.02            | Fibrin 8.06            |
| Globulin . . . . .            | 296.07           | Albumen and } 81.92    |
| Inorganic salts . . . . .     | 7.28             | extractives } 8.51     |
|                               | <hr/> 318.37     | <hr/> 98.49            |
| Sodium chloride . . . . .     |                  | 5.546                  |
| Potassium chloride . . . . .  | 3.679            | 0.359                  |
| Potassium phosphate . . . . . | 2.343            |                        |
| Potassium sulphate . . . . .  | 0.132            | 0.281                  |
| Sodium phosphate . . . . .    | 0.633            | 0.271                  |
| Soda . . . . .                | 0.341            | 1.532                  |
| Calcium phosphate . . . . .   | 0.094            | 0.298                  |
| Magnesium phosphate . . . . . | 0.060            | 0.218                  |
| Iron . . . . .                | undetermined     | ....                   |
|                               | <hr/> 7.281      | <hr/> 8.505            |

The water of the corpuscles has already been referred to. The corpuscles contain the phosphorized fats, the fatty acids being rather found in the liquor of the blood; the potash salts are also confined almost entirely to the corpuscles, there being about four times as much soda in the liquor as in the corpuscles. All of the iron of the blood is contained in the corpuscles, whereas the greater portion of the earthy phosphates is found in the liquor sanguinis. By consulting Table XLVII. the relative densities, quantity of water, solid matters, and proportion of salts in the corpuscles and liquor sanguinis may be seen somewhat in detail.

An important practical fact in reference to the red corpuscles is that their number is increased by the use of animal food and iron, but diminished by a vegetable diet. When the importance of the corpuscles is considered, it is well that the physician should bear this in mind.

<sup>1</sup> Ranke : Physiologie, S. 350. Leipzig, 1875.

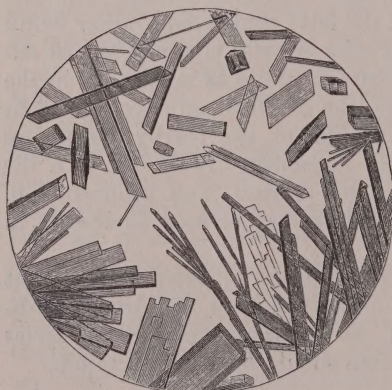
## CHAPTER XVII.

### COMPOSITION OF THE BLOOD.—(*Continued.*)

HAVING contrasted in a general way the composition of the liquor sanguinis with that of the red corpuscles, it remains for us now to consider a little more in detail the hæmoglobin of the latter, as this substance is of special interest from several points of view. When blood, drop by drop, is exposed to a cold of about  $8^{\circ}$  F., and then quickly warmed to  $68^{\circ}$  F., it will be observed that the corpuscles gradually lose their color, and that the serum becomes stained. This coloring matter from the corpuscles is capable of assuming the crystalline form, and has been indifferently called oxyhæmoglobin, hæmatocrystallin, hæmatoglobulin, hæmoglobin, and hæmatosin, though, according to some chemists, the ultimate chemical composition of these principles is slightly different.

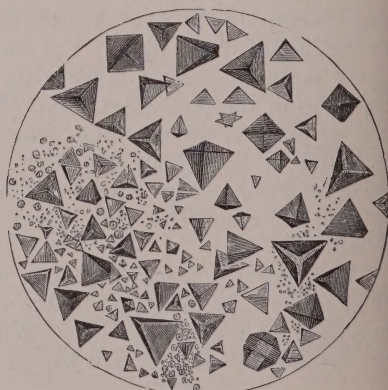
The corpuscles, left colorless by the giving up of their hæmoglobin, will retain for some time their form and elasticity, and consist largely of globulin. In this colorless condition the matter of which the corpuscles consist is generally termed the stroma. The coloring matter of the blood corpuscles, or the hæmoglobin, can be obtained in several ways. Among others, the following method, that of Preyer,<sup>1</sup> will usually give good crystals: Add enough water to a small quantity of blood free from

FIG. 123.



Prismatic crystals from human blood.  
(KIRKES.)

FIG. 124.



Tetrahedral crystals, from blood of guinea-pig.  
(KIRKES.)

fibrin, to make a clear solution and evaporate a drop under a thin cover-glass in a cool place. Should this plan fail add a little alcohol to the

<sup>1</sup> Die Blutcrystalle, S. 18. Jena, 1871.



solution and place it in a freezing mixture. Usually crystals will at once form. These crystals are more readily obtained from some animals than others—with greater facility, for example, from the blood of the dog, horse, and guinea-pig, than from that of man, and only with difficulty from that of the bat, mole, and mouse. The form of these blood crystals varies also in different animals. Thus they are prismatic in form in man (Fig. 123), tetrahedral in the guinea-pig (Fig. 124), hexagonal in the squirrel (Fig. 125).

From whatever source they are obtained they are transparent and doubly refracting, and when oxygenated exhibit the color of the blood from which they were obtained. When deoxidized, however, they alternate from red to purple or green. They are soluble in water, alkalis, and most acids; insoluble in alcohol, and will remain unchanged for some time in urine, bile.

Oxyhæmoglobin from the dog consists chemically, according to Hoppe-Seyler,<sup>1</sup> of C 53.85, H 7.32, N 16.17, O 21.84, SO 39, FeO 43.

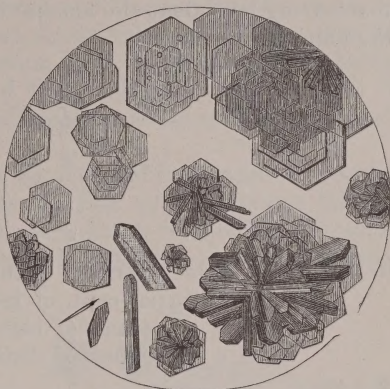
The amount of hæmoglobin present in a given quantity of blood can be determined from the amount of iron, by the spectroscope, and by colorimetric methods. The ferric method is based upon the fact that dry (100 C.) hæmoglobin contains 0.42 per cent. of iron. Knowing the amount of the latter in the blood the amount of hæmoglobin can be at once calculated by the following equation :

$$100 : 0.42 :: x : \text{Fe, } x \text{ equals } \frac{100 \text{ Fe}}{0.42},$$

in which  $x$  is the unknown quantity of hæmoglobin, Fe the known quantity of iron in the blood, and 0.42 the per cent. of iron in 100 parts of hæmoglobin. To obtain the amount of iron in the blood whose hæmoglobin is to be determined, a known quantity of blood is calcined, the ash is then treated with hydrochloric acid to obtain ferric chloride, which is then transformed into ferrous chloride by boiling with zinc until the liquid is colorless. The liquid being diluted, the amount of iron in it is determined, volumetrically<sup>2</sup> by adding from a burette permanganate of potassium in standard solution until the rose color becomes permanent after agitation, 0.0056 gramme of iron being present for each centimetre of standard solution used. The hæmoglobin, as determined from the quantity of iron (27 grammes), amounts, according to Preyer,<sup>3</sup> in human blood to about 12.34 per cent.

The spectroscopic method depends upon it having been shown by Preyer<sup>4</sup> that through a 0.8 per cent. solution of hæmoglobin the red,

FIG. 125.



Hexagonal crystals from blood of squirrel.

<sup>1</sup> Med. Chem. Unters., S. 370.  
<sup>3</sup> Op. cit., S. 117.

<sup>2</sup> Sutton: Volumetric Analysis, 4th ed., pp. 88, 94.  
<sup>4</sup> Ibid., S. 124.

yellow, and first band of the green can be seen, and that such a solution can be taken as a standard for comparison. A known amount of the blood whose hæmoglobin is to be determined is therefore diluted until the same bands are seen spectroscopically, as with the standard solution; that having been done the amount of hæmoglobin can be determined by the following equation :

$$x : k :: b + c : b$$

$$xb = k (b + c)$$

$$x = k \frac{(b + c)}{b}$$

$$x = k (1 + \frac{c}{b})$$

in which

$x$  = unknown quantity of hæmoglobin.

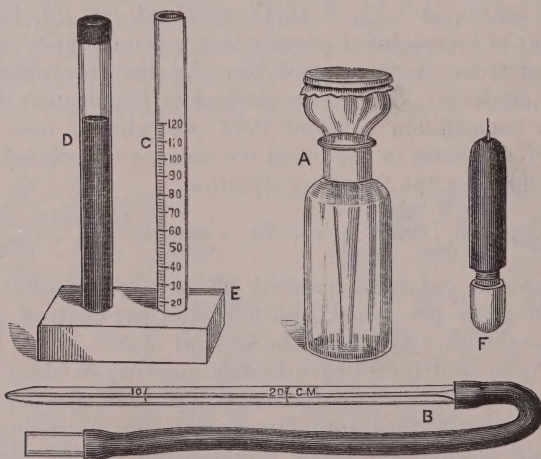
$k$  = per cent. of hæmoglobin in solution (0.8).

$b$  = volume of blood = 1 centimetre.

$c$  = volume of distilled water.

The colorimetric method depends upon the comparison of the tint of the blood to be investigated with that of a standard solution. In determining the amount of hæmoglobin in this way we make use of the hæmoglobinometer of Gowers. This consists (Fig. 126) of two glass

FIG. 126.



A. Pipette bottle for distilled water. B. Capillary pipette. C. Graduated tube. D. Tube with standard dilution. F. Lancet for pricking the finger.

tubes (D and C) of exactly the same size. Into D are placed 20 cubic mm. of blood diluted with 2000 mm. of water, the strength of the solution is therefore 1 per cent. C is graduated, the scale of 100 degrees extending over a space equal to that in D containing the 1 per cent. diluted blood. The manner of using the apparatus is as follows: Into C are placed 20 cubic mm. of the blood to be examined, which is then diluted until its color is the same as that in D. Suppose, for example,



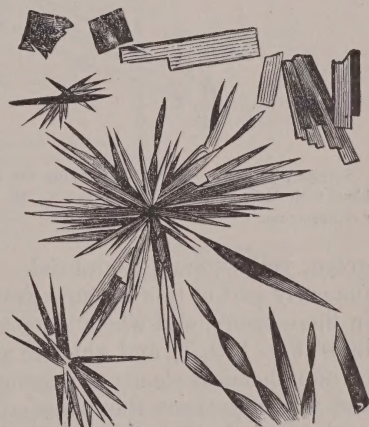
that we have to add to the blood to be investigated placed in C only 30 degrees of water (600 mm.) in order to obtain the same tint of color as that in D, instead of as in the latter case 100 degrees of water (2000 mm.), it follows that the blood in B contains only 30 per cent. of the normal quantity of hæmoglobin. Further, if the number of corpuscles in the investigated blood has also been shown to be only 60 per cent. of the normal amount, we have a fraction  $\frac{30}{60} = \frac{1}{2}$ , the numerator being the per cent. of the hæmoglobin and the denominator the per cent. of corpuscles, giving the average value of each corpuscle, or half the normal amount.

When hæmoglobin is subjected to the action of heat, acids, or caustic alkalies, its red color changes to a smutty hue, by decomposing into an albuminous substance and a colored one closely resembling bilirubin, and which has been described under the different names of hæmin, hæmatin, hæmatoin, hæmatoidin, and hæmosin, and is found in extravasations like apoplectic clots, corpora lutea, etc. (Fig. 127).

We can obtain from 100 parts of hæmoglobin, by adding hydrochloric acid, about 4 parts of hæmatin hydrochlorate,  $C_{34}H_{35}N_4FeO_5HCl$ , and 96 parts of an albuminous substance. Hæmatin is insoluble in alcohol and water but soluble in acids and alkalies, and can be obtained from a very minute portion of blood by the following method: Triturate the suspected substance with a little common salt and add glacial acetic acid, then warm the mixture till bubbles appear and then cool it. If the substance thus treated contain blood crystals of hæmatin, hydrochlorate of hæmatin will appear as rhombic tablets, disposed sometimes as stars or crosses of a red or brown color; if oxygen be added, the crystals become violet, and under

the influence of carbonic acid lose their transparency. In medico-legal questions, where there may be a very small quantity of a material to be examined, the development of hæmatin crystals will settle the question as to whether the suspected material is or is not blood, hence the importance of the method just given from this point of view. It should be mentioned, however, that while the obtaining of hæmatin as well as hæmoglobin crystals, by whatever method used, proves that the substance from which they are extracted was blood, it does not follow that it was human blood. A still more delicate means of determining the presence of hæmoglobin, and therefore of blood, is by spectrum analysis, since both the arterial and venous blood through the hæmo-

FIG. 127.

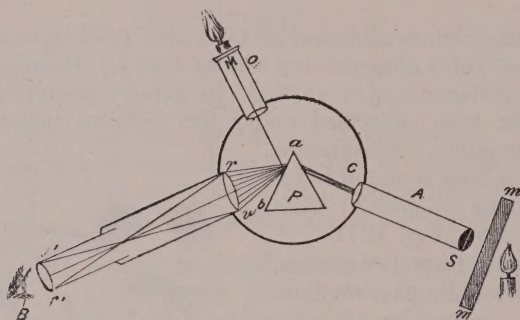


Rhombic crystals of hæmin or hydrochlorate of hæmatin, obtained by Lehman's method. They are obtained when blood is subjected to the action of a mixture of 1 part of alcohol, 4 parts of ether, and 1-16 of oxalic acid, and appear as thin brownish and brownish-green, striated, transparent crystalline laminae, often curiously twisted upon their long axes, and soon spontaneously changing into flat rhombic octahedra. (CARPENTER.)

globin they contain prevent the passage of certain rays of light, and so give rise to the dark absorption bands of the blood spectrum. In order to understand the manner in which spectrum analysis is applied to the study of the blood, let us first endeavor to explain briefly what is meant by spectrum analysis in general.

As is well known, when sunlight is transmitted through a prism, as in Fig. 128, it is decomposed into the seven colors, violet, indigo, blue,

FIG. 128.



Scheme of a spectroscope for observing the spectrum of blood. A. Tube. S. Slit *m m*. Layer of blood with flame in front of it. P. Prism. M. Scale. B. Eye of observer looking through a telescope. *v*. Spectrum.

green, yellow, orange, and red. This is called the solar spectrum. In the early part of this century Fraunhofer described certain lines situated in these colors, and which since then have been known as Fraunhofer's lines (Fig. 129, 7), and which in all probability are due to the presence of certain chemical elements existing in the form of vapor around the sun and which prevent the passage of certain rays emitted by the solar nucleus, it having been demonstrated that a vapor absorbs rays of light having the same refrangibility as that which it emits. Thus a bright yellow line in the spectrum, due to incandescent sodium, will be replaced by a dark one if the light from the burning metal be intercepted by the vapor of the same. Since then it has been shown by Brewster, Herschell, and Müller, that various colored solutions prevent the passage of certain of the rays of light, dark bands appearing in the spectrum in the place of the rays or colors arrested. In the same manner the influence of blood upon the passage of light through it was investigated spectroscopically (Fig. 128), more particularly by Hoppe-Seyler,<sup>1</sup> Stokes,<sup>2</sup> and Sorby,<sup>3</sup> and it was shown by these observers that when arterial blood is used two dark bands appear (Fig. 129, 1) between the Fraunhofer lines D and E—that is, in the yellow of the spectrum, whereas if venous blood is used only one dark band (Fig. 129, 3) appears in the yellow near the line D. Further, it was demonstrated that this difference between arterial and venous blood was solely due to whether the

<sup>1</sup> Virchow's Archiv, 1862, Band xxiii. S. 446.

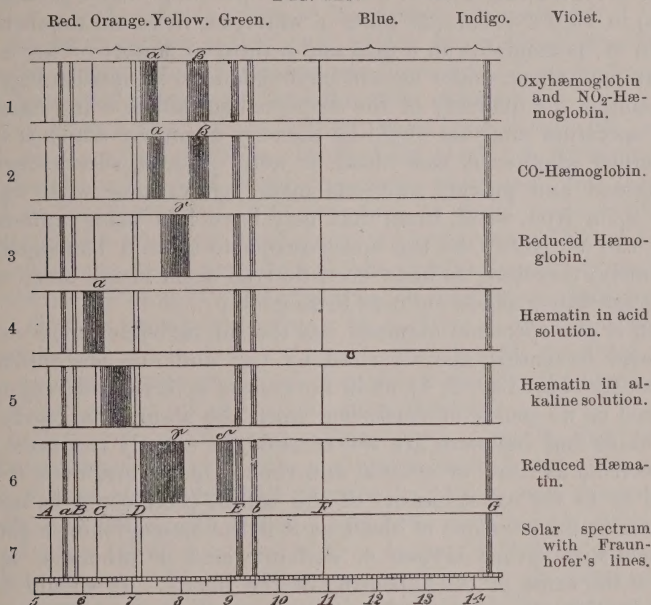
<sup>2</sup> Proc. of Royal Society London, 1863, 1864, vol. xiii. p. 355.

<sup>3</sup> Quarterly Journal of Science, 1865, vol. ii. p. 198.



coloring matter or the hæmoglobin was oxygenated or not, and that the fact of the arterial blood being red or scarlet, and of venous blood being blue or purple, was owing to oxyhæmoglobin being of a red hue and hæmoglobin of a bluish one. That the difference between arterial and

FIG. 129.



venous blood spectroscopically, and as regards color, is due simply to the hæmoglobin being oxygenated in the former case and unoxxygenated in the latter, can be readily demonstrated. Thus, if some reducing agent like ammonium sulphide or an alkaline solution of ferrous sulphate, kept from precipitation by tartaric acid, be added to arterial blood or the washings from a blood clot, the oxygen, being loosely combined with hæmoglobin, is at once seized with avidity by the reducing agent, the two dark absorption bands disappear, being replaced by the one dark band characteristic of venous blood, and the color changes from red to blue. On the other hand, with the exposure of venous blood or a solution of hæmoglobin to oxygen, or air containing such, the one dark band will disappear, being replaced by the two dark bands so characteristic of arterial blood, and the color will change from blue to red again.

According to the amount of oxyhæmoglobin present in the blood, or solution of hæmoglobin used, the dark bands will vary in extent. Thus, in a concentrated solution the two bands run into one, there being a general absorption at the blue and red ends of the spectrum, also the light then passing through only the green and red parts. With a still further increase in the strength of the solution light will be transmitted through only the red portions of the spectrum, hence its red

color, as seen by transmitted light. It is hardly necessary to add that the red rays are the last to disappear.

The extreme delicacy of spectrum analysis, as applied to the determination of the presence of blood, may be appreciated from the fact of the two bands appearing in the spectrum of light transmitted through a layer 1 centimetre thick of a solution containing only 1 gramme (15.4 grains) in 10,000 c. cm. (20 pints of water, or, in round numbers, about 1 grain of hæmoglobin in a pint and a third of water. This is an important fact, since, under certain circumstances, in medico-legal cases, for example, the quantity of the suspected substance being exceedingly small, spectrum analysis would be the only means by which it could be determined whether it was blood or not. Indeed, substances already decomposed and putrid, solutions made by washing with water, old stains upon iron, wood, linen that may have lain aside unnoticed for years, can be shown by the spectroscope to contain hæmoglobin, and necessarily, therefore, to have been derived from blood, since no other known substance affects light as hæmoglobin.

Even if the spectrum obtained was that of carbonic oxide, or hæmatoin (acid hæmatin), characterized by two and one absorption bands respectively (Fig. 129, 2, 4), as in the case of arterial and venous blood, this need be no source of confusion, since the absorption bands of carbonic oxide and hæmatin are not situated in exactly the same part of the spectrum as those of arterial and venous blood, and even if a doubt existed as to the exact locality of the bands, there could be none with reference to the presence of blood, as it is the hæmoglobin in such case, combined with either oxygen or carbonic acid, or otherwise modified, which is the cause of the appearing of the bands. It should be mentioned in this connection that spectrum analysis, like all other means at present at our command, enables us only to determine that a substance is blood, but not necessarily human blood. In examining the blood spectroscopically, while the ordinary spectroscope can be used, the microspectroscope will be found more convenient, and especially the form described by Vierordt.<sup>1</sup>

In the fact of the oxygen of the blood existing, for the most part, in a state of loose chemical combination with the hæmoglobin lies the explanation of the manner in which blood absorbs or gives off oxygen. Did the oxygen exist simply in a state of solution in the blood then the amount absorbed, or given off, would depend upon the amount of pressure present. That such is not the case, however, can be shown by exposing venous blood, containing little or no oxygen, to a succession of atmospheres containing increasing quantities of oxygen. At first there is a very rapid absorption of oxygen, but afterward this diminishes or ceases altogether. On the other hand, if arterial blood, containing a considerable quantity of oxygen, be exposed to successively diminishing pressures, at first little oxygen is given off, but afterward the escape is sudden and rapid. The amount of oxygen taken up or given off by blood is not, therefore, dependent upon pressure, except so

<sup>1</sup> Die Quantitative Spectral Analyse in ihrer Anwendung auf Physiologie. Tübingen, 1876,



far as the latter influences the passages to or from the plasma, but upon chemical affinity; the amount of oxygen absorbed, or given up by the hæmoglobin, is, therefore, a given amount, 1.76 c. cm. of oxygen for 1 gramme of hæmoglobin. In this connection it may not be inappropriate to mention that the oxygen absorbed, or given off by the hæmoglobin, has nothing to do with the oxygen entering into its molecular composition, and as already given in its chemical formula.

That the hæmoglobin is that part of the blood which absorbs and gives up the greatest part of the oxygen there can be no doubt, since, if serum freed of the corpuscles, and therefore of hæmoglobin (the latter constituting 90 per cent. of the former), be experimented with, instead of blood, little or no oxygen is absorbed, or given off, perhaps  $\frac{1}{2}$  per cent. of the entire blood, of which the serum was a part, and that proportional to the pressure. It is, therefore, to their hæmoglobin that the red corpuscles owe their function, as we have seen, of being oxygen carriers, and since the hæmoglobin at low pressure readily gives up its oxygen, the significance of this substance, in respiration, becomes very evident. In this connection it may be mentioned that the carbonic acid present in the blood does not appear to be simply dissolved there, since the absorption and giving up of carbonic acid by the blood, as in the case of oxygen, is not dependent upon pressure.

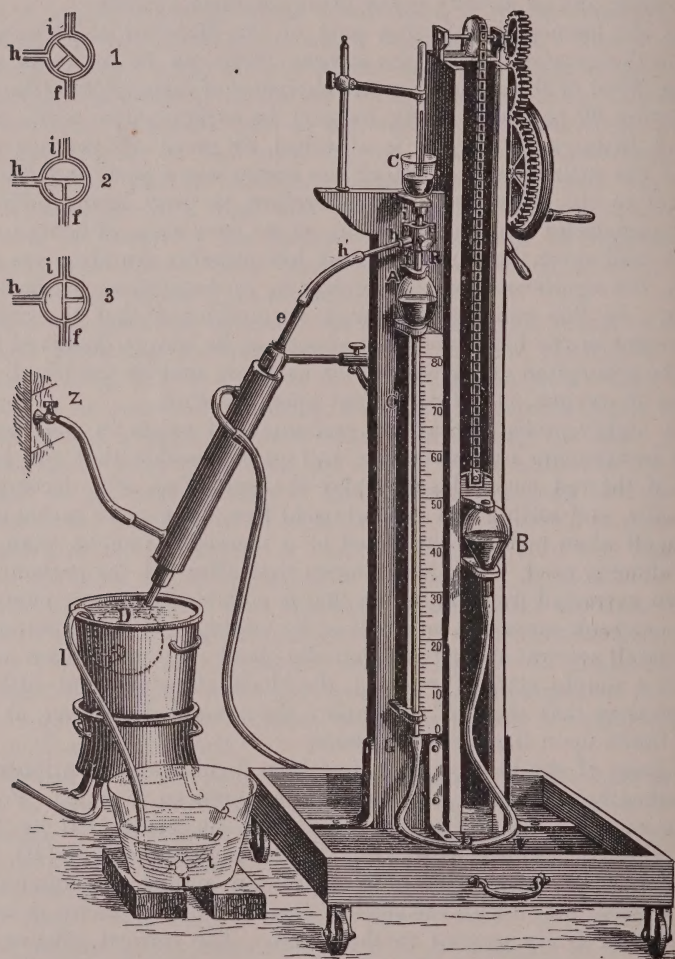
It is highly probable that the carbonic acid exists in the blood as sodium bicarbonate and carbonate, and quite possible that the hæmoglobin of the red corpuscles may play the part of an acid, decomposing these salts, and setting the carbonic acid free, since more carbonic acid is given off when blood is subjected to a mercurial vacuum than when serum alone is used. It is well known that after all the carbonic acid has been extracted from the serum that is possible by the gas pump, two to five per cent. more can be obtained by adding acid to the serum.

The small amount of nitrogen that the blood contains appears to exist there in a simple state of solution, the blood absorbing but little less nitrogen than that absorbed by water; the amount depending, at least, within limits upon the law of pressure.

The gases of the blood, as has just been incidentally mentioned, can be obtained by subjecting the blood to the mercurial vacuum. For this purpose we make use of Grehaut's gas pump, as constructed by Alvergnyat, of Paris. This consists (Fig. 130) of a glass reservoir (B), which can be lowered or raised by a rack and pinion, and which communicates by the flexible tube b with the vertical glass tube c, one metre in length, and which is firmly secured to the stand. The vertical tube expands into the oval-shaped dilatation A, which is continued upward as the narrow tube f, and whose cavity, by means of the stopcock R, can be put in communication either with that of the lateral tube h, or of the tube i terminating above in the cup C, or cut off from either. The lateral tube h is connected through tubing (h') with the stem e of the bulb D, into which is inserted a flexible tube (l) furnished with a stopcock (r), for the transference of the blood whose gases are to be determined. The stopcock (R) being in the position 1, Fig. 130—that is, all communication between the cavity of the vertical tube c

being completely cut off from that of the lateral and terminal tubes *h* and *i*, mercury is poured through the reservoir *B* until it not only rises to the level of the stopcock, but completely fills the reservoir itself. The reser-

FIG. 130.



Alvergnaud's gas pump. (BERT.)

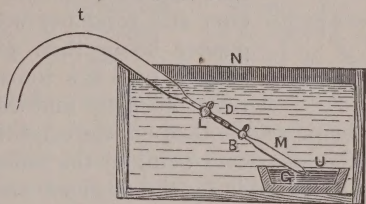
voir being then lowered the mercury will fall in the vertical tube *c*, a vacuum being produced in consequence above it. If the stopcock be now turned into the position 2 (Fig. 130), the air will pass in from the lateral tube and its appendage into the vertical tube *c*, and the mercury will fall still lower. The stopcock being now returned into the position 1 (Fig. 130), the reservoir is then elevated, and the mercury with the included air will ascend into the oval dilatation *A*. The



stopcock being now turned into the position 3 (Fig. 130), the air that was just drawn into the vertical tube *c* from the lateral tube *h* passes out of the tube *i* into the atmosphere. The stopcock is then returned to the original position (Fig. 130, 1). By depressing and elevating the reservoir *B*, and manipulating the stopcock *R* in the manner just explained, in a very short time a good vacuum is produced in the lateral tube *h h'* *e*, and its appendage *D*. A tube having been inserted into the artery or vein, the blood to be analyzed is then transferred from the vessel in the living animal to the vacuum in the following manner: A tube (*M*) of known capacity, say 50 c. c., tapering off at one end (*G*), and guarded by a stopcock (*B*) at the other, is filled with mercury by aspiration. The tube is then at the end *B* put in communication with the

bloodvessel, by means of a rubber tube readily slipping over the canula previously inserted into the vessel, which is closed by a clip. The stopcock being now opened, and the clip removed, the blood is allowed to flow away for a moment, and then (connection being made by the tubing) into the tube *M*, driving out of the latter the mercury, which can be received into a convenient receptacle. As soon as the tube is filled with blood, the stopcock being closed, connection is broken with the vessel, and the tube reversed in position, so that its tapering end *G* (Fig. 131) may be inserted into the small mercury trough *U*, previously placed in the large trough *N* containing ice-water, to retard the coagulation of the blood in the tube. The glass tube is then joined by the end *B* to the rubber tube *D* containing boiled distilled water, and previously placed over the tube *t* (Figs. 130, 131), the latter being furnished with a stopcock (Fig. 130, *r*) and leading to the vacuum. Both stopcocks (*B* and *r*) being now opened, the blood passes from the glass tube (Fig. 131, *M*) into the vacuum *D e* (Fig. 130), its place being filled with mercury from the trough; the stopcocks are then closed. The blood having passed through the tube into the bulb *D*, gives up its gases readily into the vacuum, the liberation of which is greatly facilitated by surrounding the bulb with water (Fig. 130) at a temperature of about 40° Cent. (104° Fahr.). As it is also desirable to keep back the froth and foam arising from the blood as much as possible, the lateral tube *e* is surrounded by a tin one, through which ice-cold water flows from a reservoir (*z*), and which effectually accomplishes the object. The gases having been separated from the blood, are next transferred into the vertical tube *c*, and thence through the terminal one *i* into a eudiometer, standing over mercury in the cup *C*, by depressing the mercurial reservoir *B*, and turning the stopcock *R* in the same manner as just explained. The quantity of blood from which the gases are obtained will, of course, depend upon the size of the tube transmitting the blood from the vessel to the vacuum, the vessel being clamped as soon as the tube is full of blood.

FIG. 131.



(After SANDERSON.)

In order to determine the nature and amount of the gases given off from the blood we make use of a eudiometer, slightly bent up at the end. Supposing that the gases have passed out of the pump and have displaced part of the mercury in the eudiometer, we then add caustic potash in solution, and to drive out all bubbles of air close the tube by inserting a cork through which a capillary tube passes of the shape represented in Fig. 132. The tube is then tilted, the finger being firmly placed on the top of the capillary opening, and the caustic potash makes its way up through the mercury and combines with the carbonic acid gas. The eudiometer being then placed in the mercurial trough and shaken up a few times, until the level of the mercury in the eudiometer and the trough are the same, the amount of carbonic acid is read off, the condition of the barometer and temperature of the laboratory being at the same time noted.

FIG. 132.



In determining the presence and amount of the oxygen gas we proceed in precisely the same way, only making use of a solution of pyrogallous acid instead of caustic potash. After having determined the amount of carbonic acid and oxygen, what remains in the eudiometer may practically be regarded as consisting of nitrogen. The volume of the gas obtained must be reduced, of course, to standard pressure 760 mm. mercury, and standard temperature  $0^{\circ}$  C., which can be done by the following formula:  $V = \frac{V' \times h}{760(1 + at)}$  in which  $V$  is the required volume at standard temperature  $0^{\circ}$  C. and standard pressure 760 mm.  $V'$  the volume at the observed temperature and pressure,  $h$  the observed pressure,  $a$  the coefficient of expansion, a constant (.003665), and  $t$  the observed temperature.

The formula is derived as follows. Firstly, with reference to the correction of the given volume for temperature:

$$1 + at : 1 :: V' : V \text{ or } V = \frac{V'}{1 + at}.$$

And secondly, for pressure:

$$V : \frac{V'}{1 + at} :: h : 760 \text{ or } V = \frac{V' \times h}{760(1 + at)}.$$

As an illustration of the manner of using the formula the following example will suffice. Suppose the given volume  $V'$  of gas to be corrected for temperature and pressure amounts to 30 c. c., the observed barometric pressure  $h$  being 740 mm. and the temperature  $t$  of the room  $15^{\circ}$  C.: then the required volume, or

$$V = \frac{30 \times 740}{760(1 + .003665)} = \frac{22200}{80.178200} = 27.6 \text{ c.c.}$$

that is to say, 30 c. c. of a gas, the temperature being  $15^{\circ}$  C. and the pressure 740 mm., are reduced to 27.6 c. c. at standard temperature  $0^{\circ}$  C. and pressure 760 mm.

In purely physical researches upon gases, still further corrections are



made for the tension of the aqueous vapor, and for the meniscus; the errors due to these influences are, however, so small that in physiological investigations they are usually neglected.

It will be found on an average that for 100 vol. of blood used there will be extracted by means of the mercurial pump about 60 vols. of gas, the barometric pressure being 760 mm. (30 cub. in.) and the temperature 0° C. (32° F.), and that the composition of this gas will be according to the kind of blood examined, as follows:

|                      | Oxygen.   | Carbonic acid. | Nitrogen.   |
|----------------------|-----------|----------------|-------------|
| Arterial blood . . . | 20 vol.   | 39 vol.        | 1 to 2 vol. |
| Venous blood . . .   | 8 to 12 " | 46 "           | 1 to 2 "    |

It is evident, therefore, that arterial does not differ from venous blood in containing more oxygen than carbonic acid, since there is more carbonic acid than oxygen in arterial as well as in venous blood, but in the fact that while the carbonic acid is in excess in both instances there is more oxygen in arterial than in venous blood, and more carbonic acid in venous than in arterial blood.

It will be observed, according to Table XLVIII., that there are fewer red corpuscles in arterial than in venous blood. According to some other authorities, however, the reverse is the case, the arterial containing more corpuscles than the venous blood. It must be remembered, however, that the red or blue color of the blood depends not so much upon the relative number of corpuscles present as upon the fact of the hæmoglobin of the same being oxidized or deoxidized. There are other minor differences between arterial and venous blood, as may be seen from Table XLVIII., but the essential difference depends upon the amount of oxyhæmoglobin present, the analyses of Poggiale,<sup>1</sup> Nasse,<sup>2</sup> Lehmann,<sup>3</sup> etc., showing that while there is a variability in the relative quantity of the other substances the differences are only fractional.

TABLE XLVIII.<sup>4</sup>—BLOOD.

|               | Arterial (red).                                               | Venous (blue).                         |
|---------------|---------------------------------------------------------------|----------------------------------------|
| Gases . . .   | { Oxygen 20 per cent. vol.<br>Carbonic acid 29 per cent. vol. | 10 per cent. vol.<br>46 per cent. vol. |
| Water.        |                                                               |                                        |
| Fibrin.       |                                                               |                                        |
| Extractives . | More.                                                         | Less.                                  |
| Salts.        |                                                               |                                        |
| Sugar.        |                                                               |                                        |
| Corpuscles.   |                                                               |                                        |
| Albumen . .   | Less.                                                         | More.                                  |
| Fats.         |                                                               |                                        |

The composition of the blood in the arterial system is pretty much the same throughout the body; that of the venous, however, differs considerably according to the parts and time of examination. We have already studied the blood of the splenic vein, and have seen how that of the portal is modified by admixture with that of the former and by the products of digestion, and have considered the difference in the blood of

<sup>1</sup> Comptes Rendus, 1848, t. xxvi. p. 143.

<sup>3</sup> Physiologie Chemie, Band ii. S. 203.

<sup>2</sup> Wagner: Physiologie, Band i. S. 170.

<sup>4</sup> Ranke: Physiologie, 1875, S. 358.

the hepatic vein as compared with that of the portal. The peculiarities of the blood of the pulmonary and renal veins will be deferred till the lungs and kidneys have been considered.

As the albuminous principles of the body agree essentially in their general chemical composition with each other and with the albumen of the blood and food, and as all these principles are readily transformed into each other, it is probable that the albuminous substances of the body generally, like ostein, cartilagin, globulin, etc., are derived directly or indirectly from the albumen of the blood. This view, if correct, explains why the blood contains such a large quantity of albumen, amounting to 71 parts when dry or 329 in a moist condition in 1000 parts of blood.

Generally speaking, the blood of strong, vigorous persons contains most albumen, that of weak ones the least.

The amount of albumen may in health vary slightly above or below the normal standard, but if it falls much below it is an evidence of disease. Thus there is a diminution in Bright's disease of the kidneys, where a large amount of albumen disappears from the blood, transudes through the vascular system, and escapes in the urine. As the character of albumen has been already described, I will not dwell further upon it.

There has always been and is still, a considerable difference of opinion among physiologists as to the *rôle* of fibrin in the blood; as to whether it is effete and useless, or whether it is susceptible of being elaborated into something further and useful. Among the many views that have been offered as to the nature of fibrin that of Milne Edwards is, perhaps, the most plausible. According to this distinguished physiologist, fibrin is a product of the activity of the tissues, and in normal circumstances is as rapidly destroyed as formed in the blood by the corpuscles, being burnt up by the oxygen carried by these bodies and converted into excrementitious material.

The correctness of this view can be tested by considering whether it will explain the different amount of fibrin present in the blood in the various conditions that the system may be subject to. Thus, if the theory be correct, the proportion of two to three parts of fibrin in 1000 of blood should increase or decrease as the activity of the tissues increases or decreases, the amount of the corpuscles remaining unchanged. Should the number of the corpuscles, however, diminish, the activity of the tissues remaining the same, the fibrin ought to increase in amount. If, however, the number of corpuscles diminishes at the same time that the activity of the tissues is lowered, the amount of fibrin will remain unaffected. Let us see whether these theoretical conditions are ever realized in the living animal. It is well known from the researches of pathologists, more particularly from those of Andral, that there is invariably an increase of fibrin in acute inflammations like those of pneumonia, pleurisy, diseases in which there is an excess at first of vital action in the tissues affected. On the other hand, in diseases like typhoid fever, when the vital forces are greatly prostrated, the amount of fibrin is diminished. In these diseases, at least in the early stages, the number of the corpuscles remains the same. In chlorosis, however, where the number of corpuscles is diminished, the amount of fibrin increases.



Anæmia is an illustration of the amount of fibrin remaining constant while the vital powers are lowered and the number of corpuscles diminished coincidently. This inverse ratio between the corpuscles and the fibrin is seen also in gestation, where the fibrin is increased and the corpuscles are diminished. The blood from the splenic vein is also rich in fibrin, but deficient in red corpuscles, and it is well known that repeated bleedings increase the fibrin but diminish the corpuscles. Many facts like the above, and others often apparently contradictory, illustrate this antagonism, so to speak, between the corpuscles and the fibrin.<sup>1</sup> It must be admitted, however, that in all the analyses made of the blood there are white corpuscles, etc., in the fibrin which are estimated with it, and this should be remembered when the amount of fibrin stated to have been found in an analysis is taken as the basis of a theory.

It is well known that in some cases the increase in the amount of the fibrin corresponds exactly to a diminution in that of the albumen, so that one source of the fibrin may be due to a transformation of the albumen. The very small amount of fibrin in the blood, even when estimated in the moist condition, being only then about 8 parts in the 1000, together with facts like those mentioned above, leads one to consider fibrin rather as effete matter. Still further investigation may assign some function to it as yet unknown.

The fatty matters that are found in the blood consist of serolin, cholesterin, phosphorized fats, and saponified principles like the oleates, margarates, etc. Sometimes the oleic acid exists in a free state. The fatty substances, as may be seen from Table XLIV., exist only in small quantities in the blood, and often depend upon the kind of diet. Thus fatty food increases the amount of fat in the blood. The use of these fatty substances in the blood is not exactly understood. According to some physiologists, it is thought that the fats contribute to the formation of the corpuscles, it being well known that the number of these bodies increases under the administration of cod-liver oil.

The saline materials of the blood consist of sodium, potassium, and magnesium chlorides, some free soda, of sodium and potassium carbonates, of sodium, potassium, and magnesium sulphates, of sodium, potassium, magnesium, and calcium phosphates; in a word, three chlorides, free soda, two carbonates, three sulphates, four phosphates. It is possible that these salts do not always exist in the blood in the above form, that arrangement being due perhaps to the difficult and complicated processes incidental to their analysis. It is well known that a considerable quantity of the earthy phosphates is molecularly united with the fibrin and part of the sodium chloride with the albumen. The natural relation of these salts as well as that of the others must, therefore, to a certain extent, at least, be disarranged in an analysis.

The importance of these salts is seen not only in the nutrition of the tissues, the calcium and magnesium phosphates, for example, supplying material for the production of bone, but they are also indispensable in maintaining the blood in its proper chemical and physical condition. Thus the alkalinity of the blood is due to its sodium carbonate, while

<sup>1</sup> Milne Edwards: *Op. cit.*, tome i. pp. 258-274.

the sodium phosphate dissolves the albuminous principles and inorganic matters which are insoluble in pure water. The earthy phosphates are held in solution in the serum through the presence of this salt, and to it is due the fact that so much carbonic acid is dissolved in the blood.

The existence of the corpuscles depends on the presence of sodium chloride and other salts in the serum, which, absorbing any superfluous water, prevent their dissolution. According to Milne Edwards,<sup>1</sup> the coloring matter of the corpuscles is very soluble in water, but not so in water to which have been added albumen and sodium chloride, both of which are found in the serum. While probable, yet it cannot be stated positively, that age or sex influences the quantity of these salines. There is no doubt, however, that these principles vary in quantity according to the kind of food. *And earthy* ~~An~~ exclusively animal or vegetable diet will affect the amount of ~~alkaline~~ *acid* phosphates respectively. Thus the former are most abundant in the blood of the carnivora, the latter in that of the herbivora. The proportion of the saline principles of the blood is also known to vary in disease; ~~but~~ the limited data, however, that have been collected are of more interest at present to the pathologist than to the physiologist. One of the most important substances found in the blood is iron. Indeed, when it is deficient the red corpuscles diminish in number. The normal standard is soon regained, however, when iron is administered. The iron exists in the blood combined with the coloring matter of the corpuscles; the color of the latter, though, does not depend upon the iron, as was once supposed, for the color will remain after the iron is removed, while the blood of certain invertebrates like the *Limulus* (horseshoe crab) is colorless, though iron is present. As to the exact amount of iron in the blood there is still some difference of opinion. According to Schmidt (Table XLVII.), it is still undetermined. Becquerel and Rodier give 0.5 part in the 1000 of blood, while Kuss<sup>2</sup> estimated it at 7 per cent. of the hæmatosin or hæmacrystallin or coloring matter, which would give about 7 grammes of iron (over 100 grains), there being, according to that physiologist, about 100 grammes of hæmatosin in the blood.

Various other substances are found in the blood in addition to those already mentioned, which I will consider when the subject of excretion is taken up; such are urea, uric acid, creatin, creatinin, etc.

*insoluble albumen* ~~Summing up~~, it may be said that the blood consists largely of water carrying ~~in solution~~ *and* corpuscles, albumen, salts, and excrementitious matters, and that the corpuscles are a source of power, while the albumen and salts furnish materials to the tissues, the salts, in addition, regulating the character of the blood.

In concluding this sketch of the blood a few words may be said in reference to transfusion, though this subject is usually considered as belonging to therapeutics. About the middle of the seventeenth century experiments were performed which showed that life could be saved in an animal dying from a copious hemorrhage, for example, by introducing into its vessels fresh blood from an animal of the same species. Application was soon made of this fact in the treatment of human

\* 1 Op. cit., tome i. p. 177.

2 Op. cit., p. 118.



beings, and the wildest enthusiasm was excited, great hopes being entertained that old age could be rejuvenated, etc. Several fatal cases of transfusion, however, occurring, the practice was prohibited in many places, by law. It was revived in the early part of this century, and with success. There are a number of cases on record<sup>1</sup> which would have undoubtedly proved fatal had not transfusion been used. It seems to be particularly efficacious in cases of uterine hemorrhage. When blood is transfused it should be introduced very slowly, and great caution should be exercised lest any air be mixed with it, and the quantity used be small, not exceeding three or four ounces.

Having studied the general character of the blood, let us now turn to the consideration of its circulation.

<sup>1</sup> Berard : *Physiologie*, tome iii. p. 219. Paris, 1851.

## CHAPTER XVIII.

### CIRCULATION OF THE BLOOD.

WE have seen that the use of the food is to repair the waste of the tissues, to supply fuel for the production of heat and force, and that the food is digested, absorbed, and gradually elaborated into blood. To supply the wants of the system, to furnish the tissues with material for their maintenance and repair, to carry away that which has become worn out and effete, the blood must move freely through all parts of the economy. It must circulate. By the circulation of the blood is meant that the blood moves in a circle—that is, if we follow its course, for example (Fig. 133), after it passes from the left ventricle of the heart to the aorta we shall see that the blood flows from the aorta into the arteries, thence into the capillaries, from there into the veins, from the latter by the vena cava into the right side of the heart, from the right side of the heart through the lungs back to the left side of the heart to the left ventricle, where it started.

Usually the passage of the blood from the right auricle of the heart through the lungs and left ventricle is known as the lesser, or pulmonary circulation, while the route from the left ventricle through the arteries, capillaries, and veins to the right auricle is distinguished as the greater or systemic circulation. Using the word circulation in the sense in which it is ordinarily accepted, the terms lesser and greater circulations are not appropriate, and may mislead, inasmuch as we have seen that the blood does not pass directly back from the lungs to the right auricle of the heart, whence it came, but indirectly, first coursing through the system, and that the blood flowing from the left ventricle only returns there after having passed through the lungs. There is, in this sense, then, only one circulation, however conveniently the latter may be divided into the so-called lesser and greater circulations. In another sense, however, there are innumerable circulations, greater and lesser, since the blood, after leaving the heart (Fig. 133), may go either to the head, or viscera, or extremities before returning to the heart.

As the motion of the blood is in a circle, it is immaterial at what part of the vascular system we begin its study. We shall see, however, that in exposing any of the great functions of the body, if we follow, as far as practicable, the order in which the facts were actually discovered, and the phenomena generalized by the human mind, that the subject will be presented in the most natural logical sequence. We will begin, therefore, the study of the circulation of the blood, with the demonstration of the structure and function of the heart.



## THE HEART.

The heart is a hollow pear-shaped muscular organ. It is situated in the thoracic cavity, and lies between the lungs, with which it is connected by the great bloodvessels arising from its base (Fig. 134). The

FIG. 133.

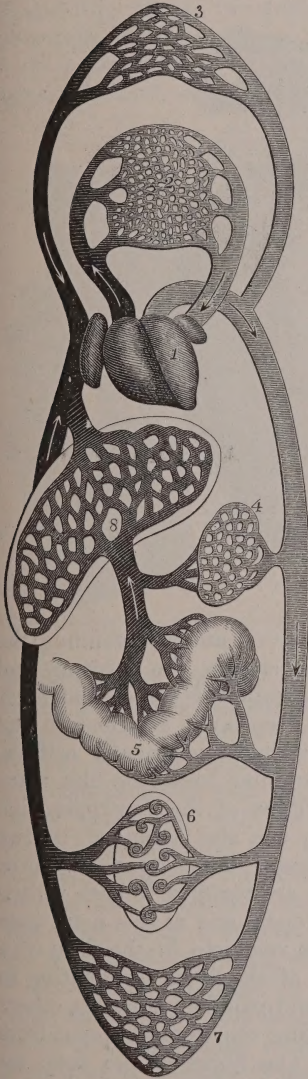
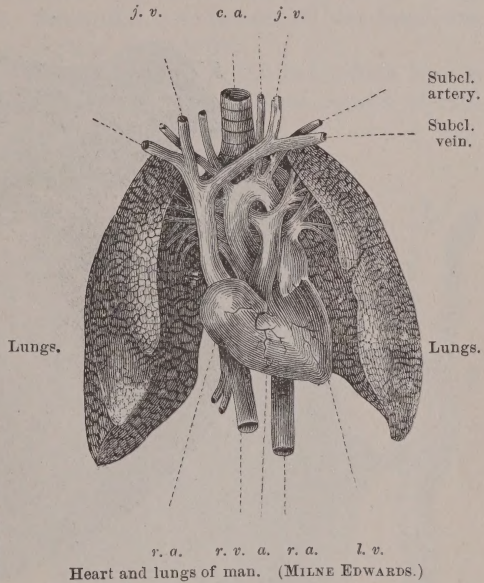


Diagram of the circulation. 1. Heart. 2. Lungs. 3. Head and upper extremities. 4. Spleen. 5. Intestine. 6. Kidney. 7. Lower extremities. 8. Liver (DALTON.)

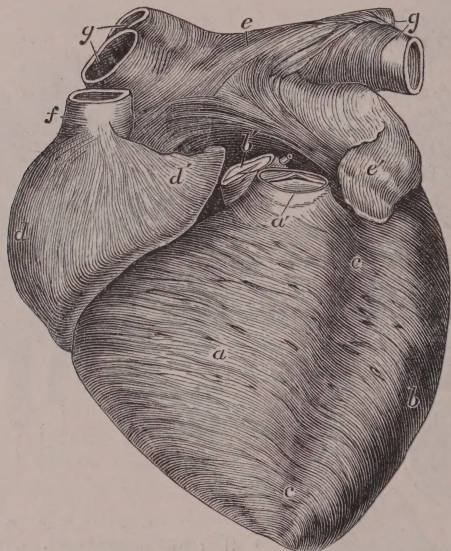
FIG. 134.



heart is loosely enclosed in a sac, the pericardium. This sac, having the form of the heart, and of a bluish-white color, consists of two layers. The external fibrous layer, continuous with the external coat of the great bloodvessels, consists of fibrous tissue, and is a strong, inextensible membrane. The internal delicate serous layer does not differ essentially in its general character from that of serous membrane. It surrounds the heart, closely adhering to it, and is then reflected over the commencement of the great bloodvessels and the interior surface of the external fibrous membrane. The cavity of the pericardium contains about a drachm or two of a serous fluid, through the presence of which the opposed internal surfaces of the pericardium glide smoothly over each other, the movements of the heart being thereby facilitated.

The pericardium is attached by connective tissue to the pleura on each side, and the tendinous centre of the diaphragm below. It is not necessary to give a detailed, minute description of the disposition of the muscular fibres of the heart, which is quite complex, a general account in connection with the present subject being sufficient. The auricles, or upper cavities of the heart (Fig. 135, *d, e*), are encircled by a thin layer

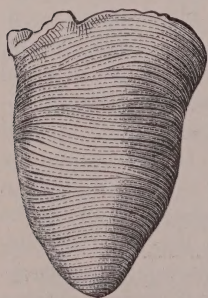
FIG. 135.



Anterior view of heart. (QUAIN)

of muscular fibres, common to both these cavities, and surrounding the auricular appendages, the entrance of the vena cava, the coronary and pulmonary veins. Beneath this superficial layer

FIG. 136.



Left ventricle of bullock's heart, showing the deep fibres. (DALTON.)

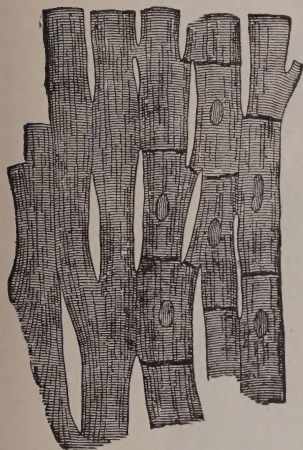
are the fibres of the deep layer attached to the fibrous rings of the auriculo-ventricular orifices, and disposed in an annular and loop-like manner. The muscular fibres of the ventricles, like those of the auricles, are also arranged in two sets, superficial and deep. The superficial fibres (Fig. 135, *a, b*), which are common to both ventricles, run from base to apex, and at this point pass into the interior of the ventricle in the form of a whorl or spiral, some of the fibres terminating in the columnæ carneæ and papillary muscles, others returning after a twisting course to the point from which they started. The fibres of the deep set (Fig. 136) surround each ventricle separately, and are disposed in a circular or transverse manner between the external and internal layers of the superficial fibres, and are much better developed in the left ventricle than in the right.



Microscopically the muscular substance of the heart consists of transverse striated muscular fibres. These fibres, however, differ from the ordinary fibres of voluntary muscles in several particulars. They are destitute of sarcolemma, much smaller and more granular, not collected into bundles, and are separated by comparatively little connective tissue. The most interesting peculiarity, however, about these fibres, is their anastomosing or inosculation with each other (Fig. 137). Their connecting fibres, no doubt, favor the contraction of the heart and thorough expulsion of the blood from its cavities.

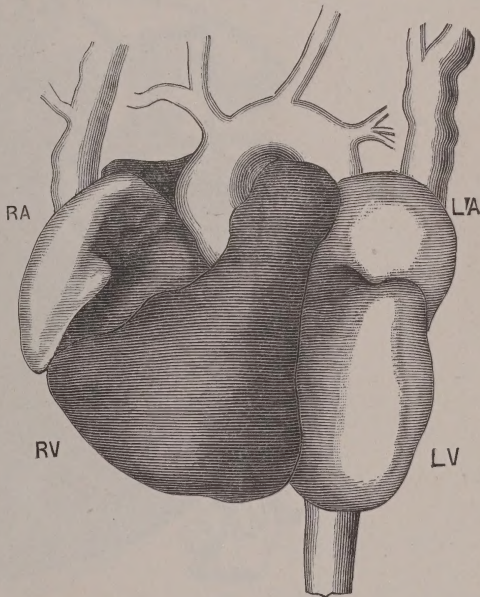
If a longitudinal section be carried through the heart from base to apex, its interior will be seen from such a section to consist of four

FIG. 137.



Muscular fibres of the heart. (QUAIN.)

FIG. 138.



Heart of manatee. RV. Right ventricle. LV. Left ventricle.

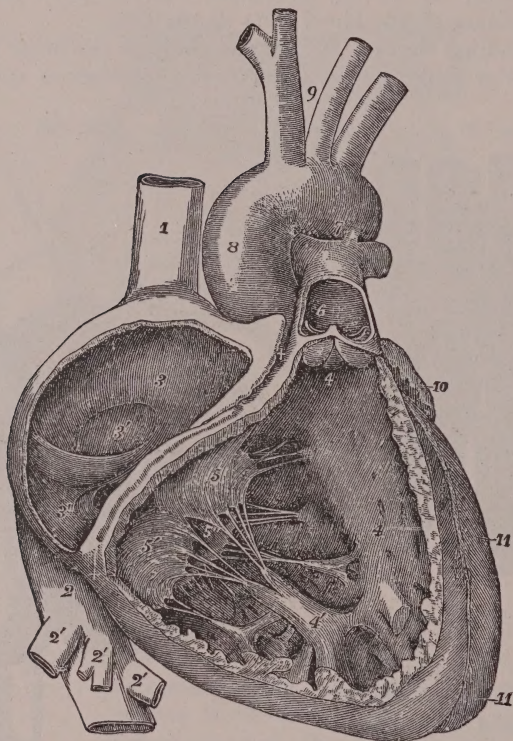
cavities: two auricles, so called from their auricular appendages, and two ventricles; that the right auricle communicates with the venæ cavæ and with the right ventricle, and the left auricle with the pulmonary veins and the left ventricle, but that there is no communication between the two auricles or between the two ventricles; the right or venous side of the heart being completely separated from the left or arterial side by the septum of the heart, which is imperforate.

In certain mammals in the dugong (halichore) and manatee (manatus) for instance, this distinction of the right from the left side of the heart is to a certain extent visible, even externally (Fig. 138), the ventricles at the apex being separated by quite an interval.

We have just seen that the heart is covered with the serous layer of the pericardium. It will be observed that the interior of the heart is also lined by a thin translucent membrane, the endocardium, which

is continuous with the internal coat of the bloodvessels and consists of a fibrous elastic and epithelial layer. Just at the point where the auricle, that of the right side, for example, passes into the ventricle, the endocardium projects into the cavity of the heart from the wall of the heart on one side, and from the septum on the other. This portion of the endocardium is strengthened by the addition of fibrous tissue.

FIG 139.



The right auricle and ventricle opened, and a part of their right and anterior walls removed so as to show their interior.  $\frac{1}{2}$ . (QUAIN.)

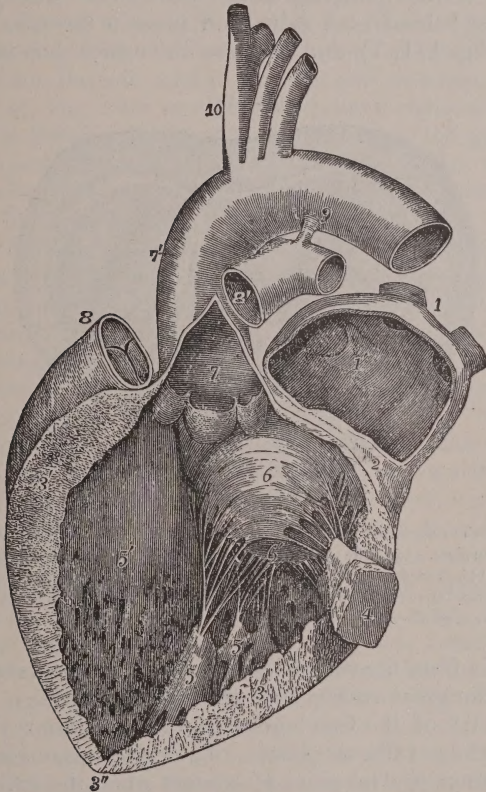
It is these projections that serve to divide the auricle from the ventricle. The interval left between these projections constitutes the auriculo-ventricular orifice. The fibro-elastic tissue in this situation forms a slight ring, to which is attached the tricuspid valve (Fig. 139, 141, 5, 5', 5''), three membranous folds, which consist of doublings of the endocardium thickened by the included fibrous tissue. By means of these curtains or valves, the auriculo-ventricular orifice can be closed, the edges of the valves being then pressed together (Fig. 141), as we shall see by the blood, and are kept stretched by the tendinous cords as the sail of a boat is kept stretched against the wind by the sheet line.

The chordæ tendineæ are tendinous cords inserted into the valve, and arise either directly from the walls of the ventricle or are connected with



it by the papillary muscles. Of these latter many pass directly again into the substance of the heart and are then known as the fleshy columns or columnæ carneæ. During the repose of the ventricle the auriculo-ventricular orifice is open, the valves then lying loosely against the walls of the ventricle. The same disposition, such as we

FIG. 140.



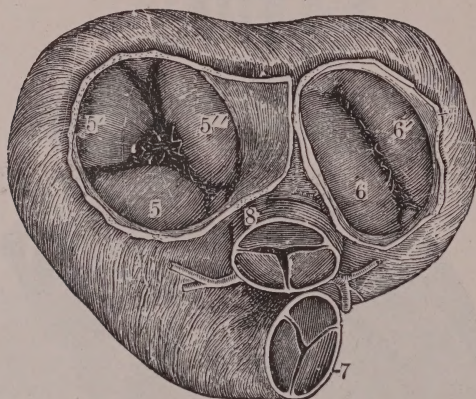
The left auricle and ventricle opened and a part of their anterior and left walls removed so as to show their interior.  $\frac{1}{2}$ . The pulmonary artery has been divided at its commencement so as to show the aorta; the opening into the left ventricle has been carried a short distance into the aorta between two of the segments of the semilunar valves; the left part of the auricle with its appendix has been removed. The right auricle has been thrown out of view. (QUAIN.)

have just described, obtains essentially in the left side of the heart. The mitral valve, however (Figs. 140 and 141, 6, 6'), by which the left auriculo-ventricular orifice is closed, consists of two membranous folds instead of three, as is the case in the tricuspid valve, and is stronger than the latter.

It will be observed that the tricuspid and mitral valves open from the auricle toward the ventricle, but do not project from the ventricle into the auricle. At the anterior angle of the base of the right ventricle (Fig. 141, 7), may be seen an orifice guarded by three crescentic

membranous folds, the semilunar valves. Through this orifice the right ventricle communicates with the pulmonary artery. The semilunar valves consist of doublings of the endocardium, strengthened by fibrous tissue. The convex border of each valve is attached to the edge of the ring-like orifice of the pulmonary artery, the free edge projecting into the latter. Behind each semilunar valve the artery is dilated into a pouch, the sinus of Valsalva. This sinus prevents the valve when open from adhering to the walls of the artery, and enables the blood to get behind each valve and press it down so that the three valves meet (Fig. 141, 7), and so close the orifice, but readily separate

FIG. 141.



View of the base of the ventricular part of the heart, showing the relative position of the arterial and auriculo-ventricular orifices.  $\frac{2}{3}$ . The muscular fibres of the ventricles are exposed by the removal of the pericardium, fat, bloodvessels, etc.; the pulmonary artery and aorta have been removed by a section made immediately beyond the attachment of the semilunar valves, and the auricles have been removed immediately above the auriculo-ventricular orifices.

when the flow is from the ventricles toward the great vessels, preventing a reflux from the great vessels back into the ventricle.

At the middle of the free border of the semilunar valves may be seen a little nodule of fibrous tissue. These nodules, or corpora Arantii serve as a common central point of contact when the valves are closed. The semilunar valves of the aorta (Fig. 141, 8) do not differ in their structure or function from those of the pulmonary artery, and, like the latter, act when in contact in closing the orifice of communication between the left ventricle and the aorta. The manner in which the tricuspid and mitral valves act can be readily demonstrated by filling the ventricles with water by means of a funnel introduced into the orifices of the pulmonary artery and aorta; the water rising up between the walls of the ventricles and the valves will float the valves up until their edges are approximated, so closing the auriculo-ventricular orifices. By pouring water into the pulmonary artery and aorta it will be seen that the water gets in between the wall of the vessel and the valve, into the sinus of Valsalva, and so forces the free edges of the semilunar valves toward each other, thus effectually closing the orifices at the mouths of the great vessels.



Such being the general structure of the heart, let us consider now the course that the blood takes in passing through it. In watching the heart beating in a living animal, a mammal, for example, it will be observed that at the same moment the right auricle is dilated by the venous blood flowing from the system through the *venæ cavæ*, the left auricle is dilated by the arterial blood flowing into it through the pulmonary veins from the lungs. This synchronous dilatation of the auricles is known as the auricular diastole. Suddenly, and succeeding this auricular diastole, or filling up of the auricles, both auricles simultaneously contract, the venous blood passing from the right auricle into the right ventricle, the arterial blood from the left auricle into the left ventricle, regurgitation to any extent into the *venæ cavæ* or pulmonary veins being prevented by the muscular fibres encircling these vessels and the pressure of the blood. This synchronous contraction of the auricles is called the auricular systole. As in the experiment just performed with the water, so the blood within the ventricles of the heart of the living animal gets in between the walls of the ventricles and the flaps of the tricuspid and mitral valves and floats the edges of the valves up until the auriculo-ventricular orifices are closed. At this moment, the ventricles being fully dilated simultaneously contract, with the effect of still more thoroughly approximating the tricuspid and mitral valves than is the case at the end of the auricular systole, and so of more completely closing the auriculo-ventricular orifices. The papillary muscles contracting at the same time as the walls of the ventricles and acting through the *chordæ tendineæ* upon the valves stiffen them and prevent their inversion into the auricles. The synchronous filling up and contraction of the ventricles is known as the diastole and systole of the heart, but more properly as the ventricular diastole and ventricular systole. During the ventricular systole the auricles are receiving blood from the *venæ cavæ* and the pulmonary veins.

Inasmuch as regurgitation backward from the ventricles into the auricles is prevented through the auriculo-ventricular orifices being closed by the approximation of the tricuspid and mitral valves during the ventricular systole, the venous blood passes from the right ventricle through the pulmonary artery to the lungs, and the arterial blood from the left ventricle through the aorta to the system. Immediately after the ventricular systole or contraction of the ventricles follows their relaxation. During this period the heart is in repose. The auriculo-ventricular orifices are again open, the venous and arterial blood that has accumulated in the right and left auricles respectively during the contraction of the ventricles and while the auriculo-ventricular orifices were closed, now flows into the ventricles, while this blood is replaced by the venous blood flowing into the right auricle from the *venæ cavæ*, and the arterial blood flowing from the pulmonary veins into the left auricle. Toward the end of the ventricular systole the venous and arterial blood, forced respectively into the pulmonary artery and the aorta, gets in between the walls of the vessels and the semilunar valves in the sinuses of *Valsalva*, and forces their free edges toward each other as in the experiment just performed with the water. At the end of the ventricular systole, the semilunar valves being closely approximated and the orifices of the

great vessels closed, through the elastic recoil of the arteries on their contents, the blood, being unable to regurgitate backward from the pulmonary artery and aorta, is forced on to the lungs and the system. It will be seen from the phenomena just described that, while the right side of the heart containing venous blood is entirely distinct from the left containing arterial, nevertheless, the two sides of the heart act as one—the venous blood flowing into the right auricle as the arterial blood flows into the left, the synchronous filling up and emptying of the auricles being followed by the synchronous dilatation and contraction of the ventricles, both ventricles relaxing together, while the blood forced out of them passes to the lungs and the system through the pulmonary artery and aorta respectively.

The beating of the heart, as we have endeavored to describe it, in an animal, a dog or a rabbit, for example, has been shown to be essentially the same in man, at least so far as comparison has been possible. As might be expected, cases of ectopia cordis are very rare, but there has been a sufficient number of such cases to demonstrate that the manner in which blood flows through the heart in man does not differ from that of other mammals.

While the action of the tricuspid valve and semilunar valves of the pulmonary artery is essentially the same as that of the mitral valve and semilunar valves of the aorta, nevertheless the valves on the right side of the heart do not close their respective orifices as perfectly as those on the left side of the heart, there being some little regurgitation possible back from the pulmonary artery to the right ventricle, and from the right ventricle to the right auricle. The effect of this insufficiency of the valves on the right side of the heart is obviously of advantage; were it otherwise, an excess of blood driven from the right ventricle through the pulmonary artery to the lungs might rupture those delicate organs. This danger is avoided through the imperfect closure of the pulmonary and the right auriculo-ventricular orifices, since, when resistance is offered by the pulmonary capillaries, the blood will regurgitate backward through the pulmonary artery to the ventricle and thence to the auricle. There is no insufficiency, however, on the left side of the heart, the auriculo-ventricular and aortic orifices being completely closed by the mitral and semilunar valves respectively. It will be observed also that the walls of the left ventricle are three or four times as thick as those of the right (see Table L.). This is due, as might have been anticipated, to the fact of the contraction of the left ventricle forcing the blood to all parts of the system, whereas the right ventricle forces the blood only to the lungs. For the same reason the walls of the auricles are thinner than those of the ventricles, little force being required to drive the blood from the former cavities into the latter.

The muscular substance of the heart, like that of muscles generally, is therefore developed according to the amount of muscular force to be expended.

As the period which elapses in mammals during a cardiac revolution—that is, the time during which all the cavities of the heart fill and empty themselves—is only about one second, actually less in man, it is evident that close and careful observation is necessary in order to dis-



tinguish the successive phenomena that we have endeavored to describe in the beating heart. It is well, therefore, to begin the study of the action of the heart by observing the phenomena, first, as they present themselves in the lower vertebrates, for example, in frogs, snakes, turtles, and alligators. Such animals are not only readily procurable, but are particularly suitable for the purpose, since in them the cardiac revolutions succeed each other much more slowly than is the case in mammals, and in the frog especially there is an appreciable interval between the systole of the auricle and that of the ventricle, whereas, in most mammals the systole of the auricle runs so into that of the ventricle that it is impossible to say exactly where the first ends and the second begins, the muscular contraction running as a continuous wave over auricle and ventricle from base to apex. Further, the heart of the frog has only one ventricle, and while there are two such cavities in the heart of the turtle, nevertheless, they communicate, the septum being but little developed. In these animals, then, the single ventricle acts like the two ventricles of the mammalian heart, and familiarizes one with the synchronous action of the ventricles when two such cavities are present. Again, these animals offer through their mode of breathing another advantage, in that the heart will continue beating even after the thorax has been opened, there being no necessity of keeping up artificial respiration. We shall see, however, when we wish to study the action of the heart in mammals, that artificial respiration must be maintained, for with the opening of the chest the lungs collapse, respiration ceases, and the circulation stops. Notwithstanding that, in mammals, a cardiac revolution occupies such a small period of time—about one second—nevertheless, the relative parts of the second elapsing during which the auricular and ventricular systole take place and the heart is in repose, have been experimentally determined, as in the horse, for example, by Marey and Chauveau.<sup>1</sup> The general results of their observations are embodied in

TABLE XLIX.—RHYTHM OF MOTION OF HEART.

| Auricular systole.     | Ventricular systole.   | Repose.                |
|------------------------|------------------------|------------------------|
| $\frac{2}{10}$ th sec. | $\frac{4}{10}$ th sec. | $\frac{4}{10}$ th sec. |

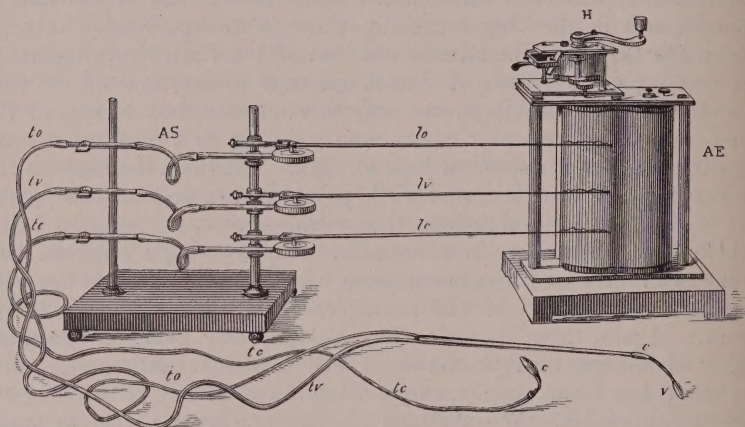
from which it will be observed that the auricular systole lasts two-tenths of a second, the ventricular systole four-tenths of a second, and the repose of the heart four-tenths of a second, one second being supposed to elapse during an entire cardiac revolution. From the observations of Franck,<sup>2</sup> made upon a woman with ectopia cordis, there is little reason to doubt that the above table represents tolerably well, also, the relative durations of the successive motions and repose of the human heart. The apparatus necessary for the above determination of the rhythm of the heart's movements as they occur in the horse, and made by Verdin, of Paris, as used by Marey, consists essentially of a sound (Fig. 142) to be introduced through the jugular vein into the heart of the animal. The sound is divided into two tubes, one of which is a distinct tube, the

<sup>1</sup> Comptes Rendus Soc. Biol., Paris, 1861. Comptes Rendus, Acad. Sciences, 1862.

<sup>2</sup> Travaux du Lab. de Marey, 1877, iii. p. 311.

other being, however, only the space around the tube. The tube terminates at one end in a little elastic bag (*v*), to be inserted into the ventricle, and at the other end in a drum provided with a registering lever (*lv*). The space surrounding the tube communicates on the one hand

FIG. 142.



Cardiograph. The instrument is composed of two principal elements: A E, the registering apparatus, and A S, the sphygmographic apparatus—that is to say, which receives, transmits, and amplifies the movements which are to be studied. The compression exerted upon the bag *c*, which is placed over the apex of the heart between the intercostal muscles, is conducted by the tube *tc*, which is filled with air, to the first lever. The compression exerted upon the bags *o* and *v*, in the double sound, is conducted by the tubes *to* and *tv* to the two remaining levers. The movements of the levers are registered simultaneously by the cylinders A E. (CHAUVEAU and MAREY.)

with a similar elastic bag (*o*) to be inserted into the auricle, and at the other end with a tube passing into a drum provided with a second similar recording lever (*lo*). The object of the elastic bags *o* and *v* is that the successive contractions of the auricle and ventricle in which they are placed will be transmitted through them to the registering levers *lo* and *lv*, and as the auricle contracts before the ventricle it is evident that the lever *lo* connected with the elastic bag (*o*) in the auricle will move before the lever (*lv*) connected with the bag (*v*) in the ventricle. If the registering levers are placed in contact with a recording surface (A E) moving at a uniform rate, and if this surface be marked by vertical parallel lines, each intervening space representing the one-tenth of a second, the lengths of time during which the auricular and ventricular systole and the repose of the heart last will be graphically recorded (Fig. 143<sup>1</sup>). The cardiac revolution in this instance lasted twelve-seconds.

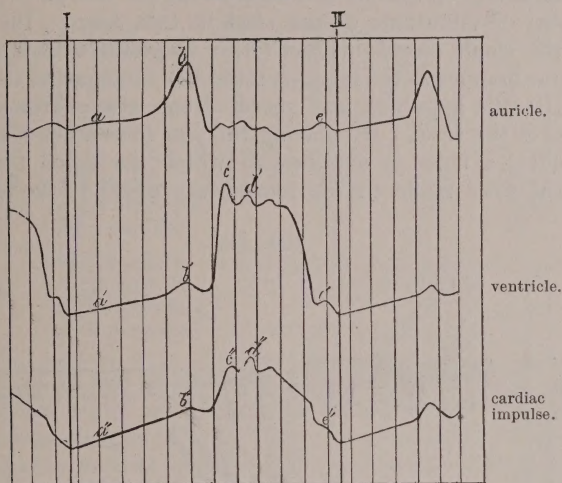
In order to divide the surface of the recording cylinder into a number of spaces each equal to the one-tenth of a second, a vibrating reed (A) and an electro-magnet (B, Fig. 144) are used. The reed clamped under the electro-magnet by one end to a stand (C), the other end dipping into mercury (D), is connected on the one hand with a battery (E), and on the

<sup>1</sup> La Circulation du Sang, p. 85. Paris, 1881.



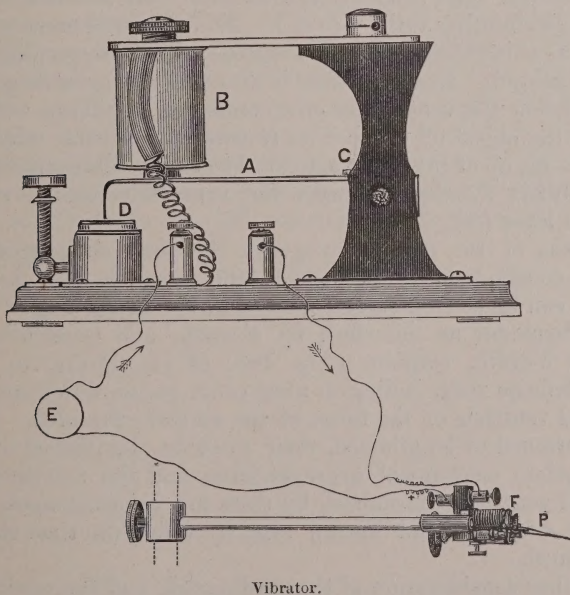
other with another small electro-magnet (F). Such being the disposition at the moment that the current is made, the electro-magnet (B)

FIG. 143.



Tracing of the variations of pressure in the right auricle and ventricle, and of the cardiac impulse, in the horse. (To be read from left to right.) (MAREY)

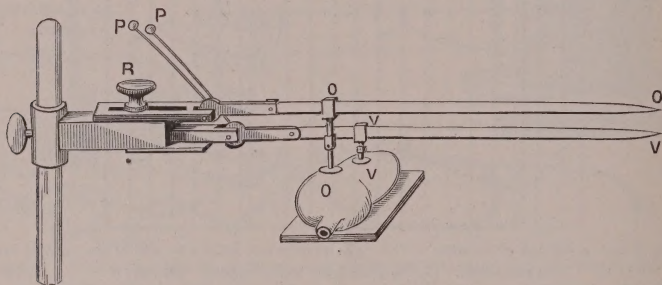
FIG. 144.



being magnetized, will attract the reed, drawing it out of the mercury; but the current being thereby broken, the electro-magnet being then

demagnetized, will cease to attract, and the reed will fall back into the mercury, remaking the current; the reed will then be again raised, the current broken, and the reed fall again into the mercury, the number of these alternate elevations and depressions per second depending upon the number of vibrations of the reed in that time. Inasmuch, however, as the small electro-magnet (F) is magnetized and demagnetized in the same manner as the large one, the bar attached to it and carrying the pen (P) will approach and recede from it synchronously with the vibrations of the reed. By placing the pen in contact with the recording cylinder, a trace is obtained in which the equal spaces between the vertical lines made by the marker are equal to the one-tenth of a

FIG. 145.



Double myograph. (VERDIN.)

second, the reed used vibrating at that rate. By substituting reeds or tuning forks vibrating at the rate of 15, 20, 50, or 100 times a second, we get traces in which the equal spaces represent the corresponding fractional parts of a second. Usually, there is also a third registering lever (Fig. 142, *lc*), below the ventricular one, connected by tubing with a cardiograph (*c*), the object of which is to transmit the cardiac impulse caused by the beating up of the heart against the chest. This impulse is shown to be absolutely synchronous with the ventricular beat as recorded by the second lever (*lv*).

By means of the double myograph the time elapsing during the successive contractions of the auricle and ventricle, and the repose of the heart, can be conveniently observed in the living frog or turtle.

The instrument as described by Franck,<sup>1</sup> and constructed for the author by Verdin, consists (Fig. 145) of two levers, to which are attached delicate rods, ending in aluminium plates, which rest upon the auricle and ventricle of the heart of the animal examined. The levers can be shortened or lengthened, their pressure diminished or increased by appropriate mechanical arrangements, and the movements of the auricle and ventricle transmitted by them are recorded upon a cylinder moving at a uniform and known rate, by which the time elapsing can be determined.

The further consideration of the cardiograph and the cardiac impulse we will defer till the next chapter, and, in concluding, call attention to

<sup>1</sup> Travaux du Lab. de Marey, t. iv. p. 407. Paris, 1877.



Table L., in which are synoptically arranged the most important anatomical facts concerning the heart having for us a functional significance.

TABLE L.—HEART.

|           |                    |                                                      |                 |                |                        |
|-----------|--------------------|------------------------------------------------------|-----------------|----------------|------------------------|
| Weight    | { in male,         | 10 to 12 ounces.                                     |                 |                |                        |
|           | { in female,       | 8 to 10 "                                            |                 |                |                        |
| Size      | { length,          | 5 inches.                                            |                 |                |                        |
|           | { breadth,         | $3\frac{1}{2}$ "                                     |                 |                |                        |
|           | { thickness,       | $2\frac{1}{2}$ "                                     |                 |                |                        |
| Thickness | { right auricle,   | 1 line.                                              |                 |                |                        |
| of walls  | { left auricle,    | $1\frac{1}{2}$ "                                     | Base.           | Middle.        | Apex.                  |
|           | { right ventricle, |                                                      | $1\frac{1}{16}$ | $1\frac{3}{8}$ | $1\frac{1}{30}$ lines. |
|           | { left ventricle,  |                                                      | $4\frac{1}{2}$  | $5\frac{1}{6}$ | $3\frac{3}{4}$ "       |
|           |                    |                                                      |                 |                |                        |
| Capacity  | { left ventricle,  | $4\frac{8}{10}$ to 7 ounces, usually 2 ounces.       |                 |                |                        |
|           | { right auricle,   | $\frac{1}{10}$ to $\frac{1}{3}$ greater than left.   |                 |                |                        |
|           | { right ventricle, | " " " " "                                            |                 |                |                        |
|           | { each ventricle,  | $\frac{1}{4}$ to $\frac{1}{3}$ greater than auricle. |                 |                |                        |

From this table it will be seen that the heart weighs, in the male sex, from ten to twelve ounces, and is heavier than in the female; that, on an average, it attains a length of five inches, and a breadth of three and one-half. It will also be noticed from the table, and, as already observed, that the walls of the ventricles are thicker than those of the auricles, while the wall of the left ventricle, on an average, may be about four times as thick as that of the right. As regards the capacity of the cavities of the heart, it might be inferred from what was said of the regurgitation of the blood backward from the lungs, that the right side of the heart is more capacious than the left; it will be seen, also, from the table, that the ventricles are more capacious than the auricles. There is still much difference of opinion as to the absolute capacity of the left ventricle. The question to determine, however, is not so much the amount of blood that the left ventricle can hold, as to what it usually does hold. This has been variously estimated at from two to seven ounces. Probably, four ounces, or a mean between these two extremes, will represent about the amount of blood that the left ventricle usually forces into the aorta at each systole.

## CHAPTER XIX.

### THE HEART.

IN examining the heart in a living animal, as described in the last chapter, it will be observed that with each ventricular systole the heart, as a whole, moves forward and upward, the apex more particularly beating up against the chest, and so giving rise to what is known as the cardiac impulse. If a finger be placed within the thoracic cavity of a living animal, between the heart and the side of the chest, with every contraction of the ventricle the finger will be pressed against the chest by the apex. Pathological cases, like that of the Viscount Montgomery, so graphically described by Harvey,<sup>1</sup> have given physiologists the opportunity of showing that the cardiac impulse is produced in men as in animals by the striking of the heart against the chest.

In man the cardiac impulse is most distinctly felt in the fifth left intercostal space, about two inches below the left nipple, and one inch to its sternal side. The force and extent to which the cardiac impulse may be perceived varies very much in different individuals, and in the same individual, according to circumstances. Thus, it is more perceptible in emaciated than in fat persons, during expiration than in inspiration, in one lying upon the left side than in one lying upon the right, etc. The movement of the heart forward and upward producing the cardiac impulse seems to be due to several causes. Thus, the sudden distention of the great elastic vessels at its base would throw the entire organ forward, the recoil of the ventricles, as they discharge their contents, further aiding the movement. The disposition of the muscular fibres is also such that the heart during its ventricular systole changes its form, bulging somewhat forward, the spiral muscular fibres, at the same time, tilting up the apex.

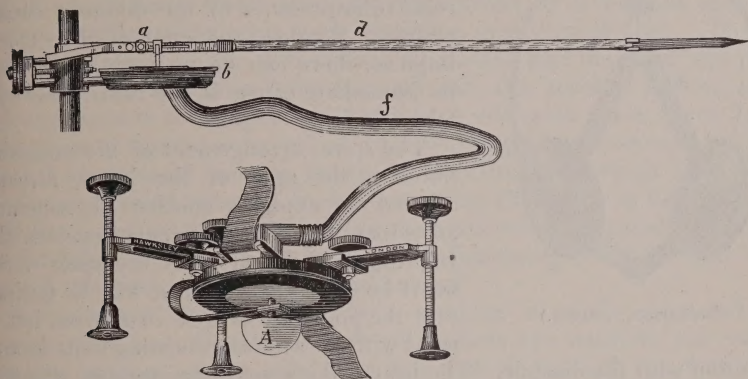
For ordinary purposes the force and extent of the cardiac impulse can be sufficiently well appreciated by the hand. The cardiograph, however, furnishes us with the means of a far more accurate study of the beat of the human heart than that afforded by the sense of touch alone. The cardiograph (Fig. 146) consists of a disk-shaped box, one side of which is formed by an elastic membrane. In the centre of the latter is inserted an ivory knob (*A*), which is applied to the chest over the place where the cardiac impulse is greatest. The box, or tympanum, communicates by an elastic tube (*f*) with a second tympanum (*b*), with which is connected a registering lever (*d*). It is evident that when the cardiograph is firmly fastened to the chest ~~that~~ the shock of the

<sup>1</sup> Exercit. de generat. Animalium, p. 156. Lond. 1651.



cardiac impulse will be transmitted to the ivory knob, thence to the first tympanum and through the column of air in the communicating tube to the interior of the second tympanum, and so, by means of the elastic and movable lid of the latter, to the registering lever. If the point of

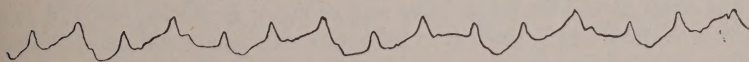
FIG. 146.



The cardiograph.

the lever be placed in contact with a cylinder revolving at a uniform rate, we obtain a graphic representation or trace of the heart's impulse (Fig. 147). By such an apparatus variations in the heart's beat, which

FIG. 147.



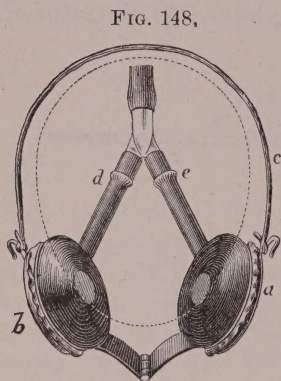
Tracing of heart's impulse in man, taken with cardiograph. To be read from left to right.

are so slight as to be quite inappreciable by the sense of touch alone, become very perceptible.

When it is desired to take a cardiographic tracing in a small animal, like a rabbit, guinea-pig, or cat, a very convenient form of cardiograph is that described by Marey<sup>1</sup> (Fig. 148), and made for the author by Verdin. The instrument consists of two tambours (*a*, *b*), each of which contains a spring, through which the membrane is kept projected. The two tambours are joined to one another pincer-like, by a hinge, and grasp the cardiac region on each side of the sternum. A girdle (*c*) attached by hooks to the tambours passes around the body of the animal, and secures the apparatus firmly. The compression of the air in the tambours due to the cardiac impulse is transmitted by the tubes (*d*, *e*) to a second tambour, to which is attached a recording lever, like that represented in Fig. 146. Fig. 149 gives the traces taken by this instrument.

<sup>1</sup> Op. cit., p. 155.

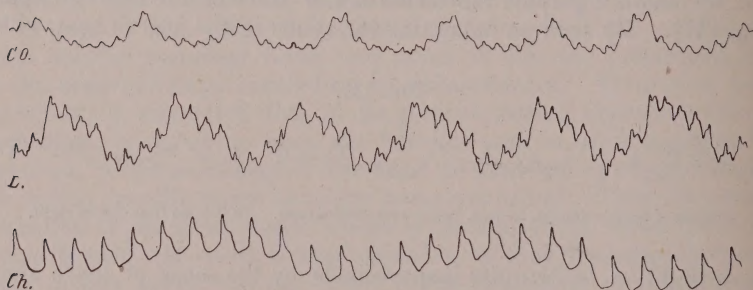
It will be remembered, that it was by means of the cardiograph and the sound introduced into the heart of the horse that Marey and Chauveau demonstrated experimentally that the cardiac impulse is absolutely synchronous with the ventricular systole. Whatever difference of opinion may exist as to the relative importance of the different causes assigned for the production of the cardiac impulse, there can be no doubt, then, that its immediate cause is the ventricular systole.



Cardiograph. (MAREY.)

The spiral arrangement of the muscular fibres at the apex of the heart, already alluded to, explains another phenomenon accompanying the ventricular systole, the twisting of the heart. If the apex of the heart be closely watched, it will be noticed that the point twists upon itself from left to right with the systole, returning to its former position with the diastole. The heart, like a voluntary muscle, which it closely resembles in its substance, also hardens during contraction. This

FIG. 149.



Tracings taken with cardiograph. Co. Guinea-pig. L. Rabbit. Ch. Cat. (MAREY.)

becomes very evident if the organ be grasped by the hand while beating. Like voluntary muscles, the heart also shortens during contraction. This can be demonstrated by quickly cutting the heart out of a living animal, pinning it down on a board by passing a needle vertically through its base, and then inserting a second needle into the board parallel with the first, so that the apex of the heart just touches the second needle. With each systole it will be seen that the ventricles invariably shorten, the apex distinctly receding from the second needle. If the beating heart be examined *in situ* there is, on the contrary, an apparent elongation of the heart during its systole. This is due, however, not to any elongation of the ventricles, but to the fact that at the moment of the cardiac impulse, which is synchronous with the ventricular



systole, the whole heart, as we have seen, is moved forward and protruded; at this moment the apex is apparently elongated, while, in reality, it is shortened.

We shall see that, on an average in man, the ventricles contract about 70 times in a minute, and assuming, as we have done, that with each systole about four ounces, or a quarter of a pound, of blood are forced into the pulmonary artery and aorta respectively, it is evident that in twenty-four hours the heart must perform a great deal of work. It can be demonstrated, as was first shown by Hales,<sup>1</sup> that the blood will rise about nine feet in a glass tube inserted into the aorta of a horse, and the experiments of Haughton,<sup>2</sup> of which we will speak again, prove that this estimate can be accepted as representing the pressure exerted by the left ventricle of man, as shown by the distance to which blood will jet from a divided artery. In demonstrating the height to which blood will rise in a glass tube inserted into the aorta we usually make use of a large turtle, which suffices very well, as illustrating the work done by the left ventricle of the heart of an animal.

In mechanics the work done by a machine is usually estimated in foot-pounds—that is, the number of pounds the machine can raise through one foot, or the number of feet that the machine can raise one pound—*i. e.*, the work equals the weight multiplied by the height. The work accomplished by the heart in twenty-four hours can be estimated approximately in the same way, and amounts to 138 foot-tons (Table L.I.)—that is, the heart performs in twenty-four hours an amount of mechanical work equivalent to that of a machine that will raise during the same time 138 tons through one foot, or 1 ton through 138 feet. If, however, we assume, as is sometimes done, that each ventricle discharges only two ounces of blood, of course the work done by the heart will be that much less; on the other hand, the work done will be greater if the ventricles are supposed to discharge more blood into the great vessels at each systole. In other words, the work done by the heart will be a maximum or minimum, according to the accepted capacity of the ventricles.

TABLE LI.

Work done by the heart in 24 hours = 138 foot-tons.

work done by the heart in 24 hours — 133 foot-tons.  
 $\frac{1}{4}$  lb. of blood expelled by left ventricle at each systole.  
 “ “ “ right “ “ “

|                    |                                                    |       |  |
|--------------------|----------------------------------------------------|-------|--|
|                    |                                                    | right |  |
| Blood flowing from | aorta into a vertical glass tube will rise 9 feet. |       |  |
| " " "              | pulmonary artery into a vertical glass tube will   |       |  |
|                    | rise 3 feet.                                       |       |  |

$$\frac{1}{4} \times 9 = \frac{9}{4} = 2\frac{1}{4} \text{ lbs. raised through 1 foot.}$$

$$\frac{1}{4} \times 3 = \frac{3}{4} = \frac{3}{4} \text{ lb.} \quad \text{“} \quad \text{“} \quad \text{“}$$

3 lbs.

$$3 \times 72 \times 60 \times 24 = 311040 \text{ lbs. in 24 hours.}$$

$$\frac{311040}{2240} = 138.8 \text{ foot-tons.}$$

<sup>1</sup> *Statistical Essays*, vol. ii, p. 11. London, 1733.

<sup>2</sup> *Animal Mechanics*, p. 137. London, 1873.

It will be observed, also, that it is assumed in man, such being essentially the case in animals, as shown experimentally by Milne Edwards,<sup>1</sup> that the right ventricle does only a fourth of the work performed by the left one.

If in a living animal the ear be applied to the precordial region, and in man more particularly to the third intercostal space a little to the left of the median line of the chest, accompanying the beat of the heart two successive sounds will be heard, followed by a silence. After a little practice it will be recognized that these two sounds differ from each other in their quality, pitch, and duration. The first sound is a dull, confused one, of a booming character, low in pitch, and lasts longer than either the second sound that follows it, or the silence intervening between the second sound and the first one. The second sound, as compared with the first one, is a clear sound, well defined, sharp, high in pitch. While, for all practical purposes, it may be said that the second sound immediately follows the first, there is quite an appreciable interval of silence between the second and the first sound, this interval of silence lasting about the same length of time as the second sound. By looking at Table LII. it will be seen that, supposing one second elapses during the period in which the first and second sounds and silence are heard, that the first sound lasts four-tenths of the second, the second sound three-tenths of a second, and the silence three-tenths of a second. It will be also observed, from Table LII., that the period of four-tenths of a second during which the first sound is heard, is absolutely synchronous with the four-tenths of a second of the ventricular systole, that the three-tenths of a second during which the second sound is heard the heart is in repose, and that the silence is synchronous partly with the last one-tenth of a second, during which the heart is in repose, and during the two-tenths of a second of the auricular systole. This comparison of the rhythm of the sounds of the heart with the rhythm of its movements, is based upon the manner in which the sounds are produced.

TABLE LII.—RHYTHM OF MOVEMENTS AND SOUNDS OF HEART DURING ONE SECOND.

| Ventricular systole.                                                                                | Repose.                                                                                                                                              | Auricular systole.                                                                                  |
|-----------------------------------------------------------------------------------------------------|------------------------------------------------------------------------------------------------------------------------------------------------------|-----------------------------------------------------------------------------------------------------|
| $\begin{array}{c} \diagup \quad \diagdown \\ 4 \\ \hline 10 \\ \diagdown \quad \diagup \end{array}$ | $\begin{array}{c} \diagup \quad \quad \quad \diagdown \\ 3 \quad + \quad 1 \\ \hline 10 \quad 10 \\ \diagdown \quad \quad \quad \diagup \end{array}$ | $\begin{array}{c} \diagup \quad \diagdown \\ 2 \\ \hline 10 \\ \diagdown \quad \diagup \end{array}$ |
| First sound.                                                                                        | Second sound.                                                                                                                                        | Silence.                                                                                            |

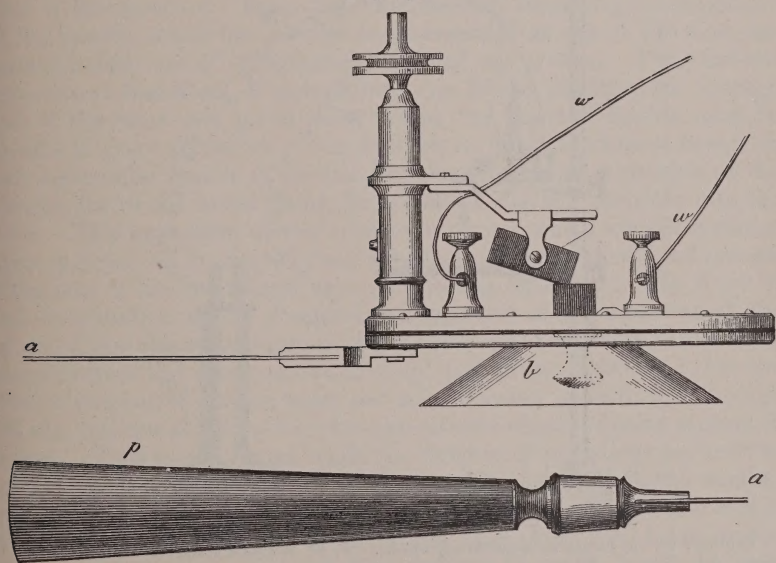
From the fact of the first sound being confused and muffled in character, one would suppose that numerous causes contribute in producing it. From Table LII. we see that the first sound is heard, and lasts during the ventricular systole; now at the moment the auriculo-ventricular valves flap together their movement must be then one cause of the first sound of the heart, and accounts for its valvular element. That the closure of the auriculo-ventricular valve contributes in the produc-

<sup>1</sup> Physiologie, tome iii. p. 118.



tion of the first sound can be further demonstrated by experiments like those of Chauveau and Faivre,<sup>1</sup> who either modified the first sound or abolished it altogether by preventing the closure of these valves by cutting the chordæ tendineæ, or introducing a wire ring into the auriculo-ventricular orifices. Further, pathology shows that, in man, the character of the first sound is changed if the auriculo-ventricular valves are diseased, and it is well known, also, that in auscultation the first sound is heard with its maximum intensity over these valves, and that it is propagated downward along the ventricles to which they are attached toward the apex. It is well known, and readily shown by the application of the myophonic telephone (Fig. 150), that when a muscle contracts, being thrown into vibration, a sound is produced; now, as the ventricular systole is caused by the contraction of the muscular fibres of the ventricle, at this moment a sound will be produced which,

FIG. 150.



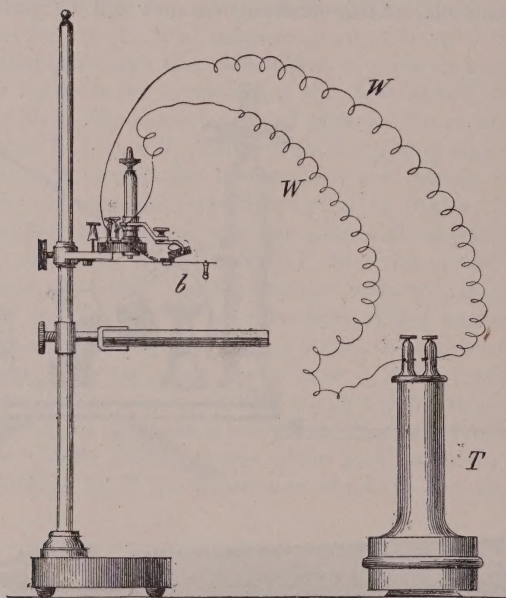
Helmoltz's myophone. *b.* Button to be placed on muscle. *p.* Handle. *w, w.* Wires for attachment to telephone.

in the case of the frog, can be made audible by the cardiophonic telephone (Fig. 151), and which contributes undoubtedly, in man, to the production of the first sound. Finally, the beating up of the heart against the chest in itself is partly a cause of the first sound. There appear, then, to be three distinct causes, each contributing in the production of the first sound. First, the closure of the auriculo-ventricular valves; second, the muscular contraction; third, the cardiac impulse—hence the confused, muffled character of the first sound of the heart. As has already been observed, the second sound differs from the first in being a clear, well-defined sound, and is essentially of a valvular character. It

<sup>1</sup> Nouvelle recherches experimentales sur les Mouvements du Cœur, etc., p. 30. Paris, 1856.

is heard (see Table LIII.) during the first three-quarters of the period in which the heart is in repose. Now, at this moment the semilunar valves of the pulmonary artery and aorta are flapping together through the blood getting in between the valves and the walls of the vessels. The closure of these valves will account for the second sound of the heart and its simple valvular character. The second sound of the heart can be imitated by suddenly closing the aortic valves by a column of water, as was first shown by Rouanet,<sup>1</sup> and can be abolished by hooking back the semilunar valves in a living animal, as was first demonstrated by Williams,<sup>2</sup> and confirmed by the Dublin Committee in their report presented to the meeting of the British Association in 1836. Finally,

FIG. 151.



Cardiophone. *b.* Button to be placed upon heart. *W, W.* Wires for attachment to telephone. *T.* Telephone.

the period of silence coincides with the last one-tenth of a second of the period of repose, and the two-tenths of a second during which the auricles silently contract.

We learn also through the changes produced in the character of the second sound of the heart from disease of the semilunar valves, and from auscultation that the second sound is heard most distinctly opposite the semilunar valves, and is propagated upward along the great vessels to which they are attached. There can be no doubt, then, that the second sound of the heart is caused simply by the closure of the semilunar valves of the pulmonary artery and aorta.

<sup>1</sup> Cyclopædia of Anat. and Phys., vol. ii, p. 617.

<sup>2</sup> Ibid., p. 618.



TABLE LIII.—POSITION OF VALVES OF HEART.

|                 |                                                                  |
|-----------------|------------------------------------------------------------------|
| Aortic.         | Opposite third intercostal space on left side, close to sternum. |
| 2d. Pulmonary.  | Opposite junction of third rib with the sternum.                 |
| 3d. Mitral.     | Opposite third intercostal space one inch to left of sternum.    |
| 1st. Tricuspid. | Behind middle of sternum at level of fourth rib.                 |

The great practical importance to the physician of a thorough knowledge of the manner in which the sounds of the heart are produced, and of the position of the valves in reference to the walls of the chest, as aiding him in diagnosing diseases of the heart, is so obvious that it will not be considered superfluous in attention being called to the topographical anatomy of the valves as given in Table LIII.

When it is considered that age, sex, food, exercise, etc., influence the rapidity of the action of the heart, it becomes evident that an intimate sympathy must exist between the circulation and the other great functions of the economy. From time immemorial, therefore, the frequency of the heart's action has always been regarded as one of the most important indications of the general health of the system. The practical importance, therefore, of determining, as far as possible, the average beat of the heart in a given time, within the limits of health, must be obvious to every physician. We shall see in the next chapter that with each ventricular systole or cardiac impulse there is an expansion of the arteries due to the blood being forced out of the left ventricle into the aorta. This expansion of the arteries or pulse, which we will consider again in detail, is, for convenience' sake, usually felt and counted instead of the beat of the heart itself, and, other things being equal, the result of such examination can be accepted as a criterion of the condition of the heart and vascular system generally. It will be observed from Table LIV., compiled from the observations of Guy<sup>1</sup> and Milne Edwards,<sup>2</sup> that the average number of cardiac beats per minute varies according to the age and sex, and this should always be remembered when the pulse is counted in man. Thus in the fœtus, while the number of pulsations per minute is 140 (determined by listening to the fœtal heart), at birth the number falls to 136, and that up to the third year of life, while the pulse is still the same in both sexes, it now averages only about 107 beats to the minute. As we pass, however, from infancy to youth, it will be seen that the number of pulsations per minute gradually diminishes, and that at the same period the pulse of the female is a little quicker than that of the male. In adult life the average number of pulsations in the male may be said to be from 70 to 72 per minute, and from 6 to 8 beats more in the female. At the approach of old age the pulse becomes a little more frequent, at eighty years of age the number of beats usually being about 80 a minute.

<sup>1</sup> Cyclopædia of Anat. and Phys., vol. iv. p. 181.

<sup>2</sup> Physiologie, tome iv. p. 62.

TABLE LIV.—FREQUENCY OF HEART'S ACTION.

| Age.                   | Pulsations per minute. |         |
|------------------------|------------------------|---------|
|                        | Male.                  | Female. |
| Fœtal. . . . .         | 140                    | 140     |
| At birth . . . . .     | 136 <sup>1</sup>       | 136     |
| 1 year . . . . .       | 128                    | 128     |
| 2 years . . . . .      | 107                    | 107     |
| 2 to 7 years . . . . . | 97                     | 98      |
| 8 " 14 " . . . . .     | 84                     | 94      |
| 14 " 21 " . . . . .    | 76                     | 82      |
| 21 " 28 " . . . . .    | 73                     | 80      |
| 28 " 35 " . . . . .    | 70                     | 78      |
| 35 " 42 " . . . . .    | 68                     | 78      |
| 42 " 49 " . . . . .    | 70                     | 77      |
| 49 " 56 " . . . . .    | 67 <sup>2</sup>        | 76      |
| 56 " 63 " . . . . .    | 68                     | 77      |
| 63 " 70 " . . . . .    | 70                     | 78      |
| 70 " 77 " . . . . .    | 67                     | 81      |
| 77 " 84 " . . . . .    | 71                     | 82      |

As is well known, in animals of different species, but which are closely allied in their general organization, the pulse varies with the size of the animal, being slowest in the largest and fastest in the smallest animals. Thus in the horse the number of beats is only 40 to the minute, in the ass about 50, in the sheep from 60 to 80, in the dog 100 to 120, in the rabbit 150, and in some of the smallest rodents even 175. The circulation is also more rapid in small insects than in large ones, and it has long been a matter of observation that in man the pulse is slower in persons of large stature than in those of small. This connection between the rapidity of the pulse and the size of the animal seems to be a very general one in the animal kingdom, so far as has been observed, and its significance will become apparent when we study the production of animal heat in the economy, for we shall see then that the rapidity of the circulation is directly correlated with the production of heat and force, and that, as a general rule, the greatest amount of nervo-muscular activity is exhibited by the smallest animals of any one order rather than by the largest ones.

This dependence of the pulse on the size may to a certain extent explain the difference between the pulse of the young and of the old, and of the sexes as just given in Table LIV., but it should be remembered that the observations of Volkmann<sup>1</sup> show that youth and sex in themselves, without regard to size, influence the rate of the pulse, for in individuals of equal size the youngest had the quickest pulse, and the pulse of the woman was always quicker than that of the male.

It must not be forgotten, however, in counting the pulse that often individuals are met with in perfect health in whom the pulse is extremely rapid, or just the reverse. Thus, according to the late Prof. Dunglison,<sup>2</sup> the pulse of Sir William Congreve never fell below 128 beats per minute, while, as is well known, on the other hand, that of Napoleon I. often did not exceed 40 beats to the minute.<sup>3</sup> Haller<sup>4</sup> refers to cases where the pulse was still slower, being only 23 beats to the minute.

<sup>1</sup> Die Hæmodynamik, S. 30, 36. Leipzig, 1850.

<sup>3</sup> Berard : Physiologie, tome iv. p. 113.

<sup>2</sup> Human Physiology, 1856, 8th ed., vol. i. p. 446.

<sup>4</sup> Elementa Physiologia, tome ii. p. 256.



Among the six hundred gentlemen who have annually honored the author in attending his lectures, there have been several instances in which almost as marked a difference in the beat of the pulse was observed as in that of the two celebrated cases first referred to. Idiosyncrasy may, therefore, have a greater influence in modifying the beat of the pulse than is usually assigned to it.

As is well known, the action of the heart is also influenced by digestion; according to Milne Edwards,<sup>1</sup> there is an increase of from five to ten beats after each meal. On the other hand, prolonged fasting diminishes the frequency of the pulse from twelve to sixteen beats. According to the same high authority, while vegetable food diminishes the action of the heart animal food increases it, fermented drinks at first diminish then accelerate the movements of the heart. Coffee is, however, in the highest degree a cardiac stimulant. Every one is familiar with the fact that any violent exercise, like running or jumping, increases the action of the heart. As long ago as the early part of the last century it was shown, by the experiments of Bryan Robinson,<sup>2</sup> that the pulse of a man in the recumbent position being 64 to the minute, was increased to 78 during a slow walk, and still further increased to 100 by walking a league and a half in an hour, and rose as high as 140 to 150 after running as rapidly as possible. It is also well known, from the experiments of Guy,<sup>3</sup> that if the number of pulsations on the average be 66 to the minute in a man lying down, the number will be increased to 71 if he sits up, and will be still further increased to 81 if he stands up. After what has just been said in reference to muscular activity increasing the action of the heart, the results of Guy's experiments are just what might have been expected, since muscular force is developed in changing the position of the body and maintaining it in equilibrium.

Indeed, it was in this way that many of the older physiologists theoretically explained the acceleration of the heart's beat observed in the change of posture just referred to. It was Guy, however, who first demonstrated, by means of a revolving board which supported the person who was the subject of the experiment and so relieved him of the necessity of supporting himself by muscular exertion, that the variations in the frequency of the heart, according to the position of the body, was dependent upon the quantity of muscular force put forth in maintaining equilibrium in each of the positions. The practical importance of these facts for the physician cannot be exaggerated, since it is obvious that, in a person suffering with heart disease, it is of the utmost importance that any increase in the action of the heart should be avoided. The greatest caution, under such circumstances, should be advised in the taking of exercise; any sudden or violent effort, like quickly lifting up a trunk, or running rapidly up stairs, should be strictly prohibited, the slight acceleration in the heart's beat from such an effort being frequently a cause of death in persons affected with heart disease.

It is well known that during the day there is a variation in the action of the heart, and for a long time it was supposed that the pulse was

<sup>1</sup> Physiologie, tome iv. p. 79.

<sup>2</sup> A Treatise on the Animal Economy, p. 177. Dublin, 1732.

<sup>3</sup> Cyclopædia of Anat. and Phys., vol. iv. p. 188.

quicker in the evening than in the morning. According to the older physiologists, "*Pulsus nocturnus multo celerior est.*"<sup>1</sup> When, however, the action of the heart at evening is considered uninfluenced by food, exercise, etc., it has been found that the pulse at that period of the day is really slower than in the morning, and that the heart is less susceptible to the action of stimulants. This condition is due, no doubt, to muscular fatigue.

In sick persons, however, it is otherwise, since at evening there is usually some fever present, and this is accompanied by a quicker pulse. According to Milne Edwards,<sup>2</sup> while sleep tends to diminish the action of the heart, the number of pulsations, at least in man, is not diminished to any extent by that circumstance. In women, and especially children, in that condition, however, there seems to be considerable difference as compared with the wakeful state. The temperature of the surrounding atmosphere influences also the rapidity of the action of the heart—heat increasing and cold diminishing the number of heart beats.

De la Roche<sup>3</sup> found that his pulse was increased to 160 beats per minute in an atmosphere of 150° Fahr., and it is well known that the pulse is quicker in hot countries than in cold ones. Among the other influences that accelerate or diminish the action of the heart must be mentioned the condition of the respiration. When the manner in which the blood flows through the pulmonic capillaries, and the changes produced in it, have been described, the mutual sympathy existing between the heart and lungs will then be fully appreciated. It would be anticipating too much to give a detailed account of this mutual influence at present; a few words now, therefore, will suffice. If the heart ceases to beat, the muscles involved in respiration not receiving their accustomed amount of fresh blood, lose their contractility, will not respond to their natural stimuli, and respiration ceases. On the other hand, if respiration ceases first, the heart soon stops beating. This is due to the fact that unaërated blood will not flow through the systemic capillaries, and that, in consequence, the whole arterial system becomes gorged with black blood that has flown from the right side of the heart through the lungs back to the left side of the heart, and so into the aorta unaërated. While at first under such circumstances the heart will continue to contract, forcing the blood into the great vessels, soon the resistance offered by the engorged state of the pulmonary capillaries and the arterial system becomes so great that the heart can no longer empty its cavities; it then becomes enormously distended with unaërated blood, such distention finally producing a paralysis of the muscular fibres of the heart, and so arresting its action. Such a condition of things is well seen in cases of death from asphyxia. The influence of the cessation of respiration as a cause of the arrest of the heart's action, also, by the mere pressure of the air enclosed within the chest upon the heart, has been more than once demonstrated in man, and sometimes probably fatally. Thus, by closing the mouth and con-

<sup>1</sup> Keill: *Teutamina medico-physica*, p. 178. Lond. 1730.

<sup>2</sup> *Physiologie*, tome iv. p. 74.

<sup>3</sup> These, Paris, 1806, p. 33.



tracting the walls of the chest simultaneously, respiration can be voluntarily suspended, with the effect of diminishing the action of the heart, and even of stopping it entirely. By suspending his respiration and contracting forcibly at the same time the walls of the chest, Prof. E. F. Weber, of Leipsic, was able to diminish the cardiac beats to three to five a minute, which were unaccompanied with the cardiac impulse or sounds, and with the result, finally, of stopping the action of the heart altogether. On one occasion, having suspended his respiration longer than usual, Professor Weber<sup>1</sup> fell into a syncope. This case, concerning the truth of which there can be no question, confirms the statements made by Galen,<sup>2</sup> and others, that death in certain individuals had been caused by the voluntary suspension of their breathing. One of the most interesting and best authenticated cases of the possibility of temporarily arresting the action of the heart was that of Colonel Townsend, reported in the early part of the last century by Cheyne.<sup>3</sup> This physician relates how Colonel Townsend could so arrest the breathing and the beating of his heart that death was simulated. In this condition the pulse could not be felt at the wrist; there was no cardiac impulse; a mirror placed in front of the mouth was not tarnished, and, apparently, he was dead. On the occasion reported by Cheyne, Colonel Townsend remained in this condition for half an hour; gradually, however, the respiration and circulation became reëstablished. It should be mentioned, however, that Colonel Townsend died later in the afternoon of the same day that the facts just described occurred.

Having described the motion of the heart and the various influences that modify it, it remains for us now to consider what is known of the cause of this motion. When we come to the special study of muscular contractility we shall learn that an ordinary voluntary muscle usually contracts in response to a stimulus, the will emanating in the brain and transmitted through a nerve to the muscle.

While the heart is a muscular organ, its action differs from that of the ordinary muscle in being involuntary in character. The voluntary muscle, however, not only contracts through the influence of the will or nerve force, but also in response to mechanical, electrical, or chemical stimuli, and, in this respect, the heart does the same. Thus, if the chest of a living animal be opened, and the heart mechanically irritated by an instrument, a scalpel, for example, it will be seen to contract like any other muscle stimulated in a similar manner. The same effect follows the application of electricity by means of the electrodes. The addition of warm water, and exposure to the air will also cause the heart to contract. A significant fact to be noticed in all of these experiments is that the effect of the stimulus is much greater when it is applied to the inner rather than to the outer surface of the heart, and that, even after the outer surface of the heart has ceased to respond to stimuli the inner surface will.

The muscular substance of the heart, then, like that of any other muscular organ is endowed with the property of contractility, through

<sup>1</sup> Milne Edwards: *Physiologie*, tome iv. p. 88.

<sup>2</sup> *Œuvres trad. de Daremberg*, tome i. p. 366.

<sup>3</sup> *The English Malady*, p. 307. London, 1734.

which the organ contracts in response to various stimuli. The nature of this property of muscular substance, contractility, and its relation to stimuli, will be considered hereafter. Of the different kinds of stimuli that are known to produce contraction of the heart, none are so important as the contact of blood with the inner wall of its cavities. Indeed, since the time of Haller, the presence of blood within the cavities of the heart has been regarded as an indispensable condition in the production of its contractions, if not the cause itself. While there were physiologists, prior to the time of Haller, who held this view, it is to that physiologist that science is indebted for most of the facts that can be brought forward even now in support of it. Among the many experiments performed by Haller<sup>1</sup> may be mentioned the following striking ones. The vena cava and the branchial artery being ligated in an eel by the contraction of the auricle the blood was forced into the ventricle, and the auricle not receiving any more blood through the ligation of the vena cava soon ceased to beat. On the other hand, the ventricle being unable to empty itself entirely, the branchial artery being tied, continued to dilate and contract. When, however, the ligature was removed from the vena cava the auricle began to beat again.

In another experiment, performed on a cat,<sup>2</sup> the superior vena cava was divided, and the inferior vena cava ligated, with the effect of cutting off the supply of blood to the right auricle; then the pulmonary artery was opened and the right ventricle consequently emptied. On the other hand, by the ligating of the aorta the blood was retained in the left ventricle. It was observed that the right auricle soon ceased to beat, then the left ventricle, whereas the left ventricle continued to beat for four hours.

To appreciate fully the importance of these experiments, particularly the latter, it must be remembered that usually the right auricle is the last part of the heart to cease beating, and that the left ventricle stops beating before the right, whereas, in the experiment just described, exactly the reverse was the case.

These experiments prove, therefore, the importance of the presence of blood in the cavities of the heart as an indispensable condition in producing its contraction. It is also well known that when an animal is dying of hemorrhage, and the heart has stopped beating, the introduction of a little fresh blood by transfusion will reëstablish its movements. Further, when the heart is taken entirely out of an animal, a frog, for example, and completely emptied of blood, with the effect of stopping the beat, the contractions will recommence with the introduction of a few drops of blood into the ventricle. Even fragments of the heart can be made to contract and dilate by the addition of a few drops of blood. It appears, then, from experiments of this kind that the most important cause of the movement of the heart is the presence of blood in its cavities.

The stimulating effect of the blood, however, is not limited to the interior of the heart, for with each ventricular systole blood is forced

<sup>1</sup> *Mémoires sur la Nature Sensible et Irritable des Parties du corps animal* a Lausanne, 1756, tome i. p. 370.

<sup>2</sup> *Op. cit.*, tome i. p. 363.



through the aorta into the coronary arteries, and thence into the substance of the heart, and this blood will act as a stimulus to the external parts of the heart, just as we have seen the blood acts as a stimulant to the internal ones. During the systole of the heart, however, the minute vessels being compressed by the contracted muscular fibres the flow of the blood will be limited principally to the superficial parts of the heart, so that it is during the diastole rather that the coronary capillaries receive blood. This view does not imply, as held by Brucke,<sup>1</sup> that the orifices of the coronary <sup>arteries</sup> ~~orifices~~ are closed by the semilunar valves of the aorta during the ventricular systole, and that these vessels are filled during the diastole, for, as Hyrtl<sup>2</sup> demonstrated, the coronary arteries are filled during the ventricular systole, but only supposes that the coronary capillaries receive their maximum amount of blood during the diastole. The filling up of these interstitial vessels is, therefore, coincident with the filling up of the cavities of the heart itself.

The stimulus is, therefore, exerted by the blood simultaneously upon the inner and outer parts of the heart. The importance of the blood flowing through the coronary system of vessels, not only as contributing a part of the stimulus necessary for the heart's action, but of furnishing its muscular substance with fresh material for the elaboration of muscular or contractile force, is well seen when the coronary arteries are ligated, the effect of which, as Erichsen<sup>3</sup> showed, is to stop almost immediately the beating of the heart. According to Brown-Séquard,<sup>4</sup> while the arterial blood in the coronary vessels furnishes the nutritive materials out of which the muscular or contractile force of the heart is developed, the venous blood, on account of the carbonic acid it contains, supplies the necessary stimulus to excite this force, carbonic acid being a stimulus to muscular contractility. If this view be accepted, it offers, perhaps, an explanation of the fact, already referred to, that the right auricle is the last part of the heart to cease beating, and that the left ventricle stops beating before the right, as the stimulating effect of the venous blood on the right side of the heart will last longer than that of the arterial blood on the left side on account of its containing more carbonic acid. There must be taken into consideration also in studying the action of the heart, as we shall soon see, that as blood is flowing into the aorta during the ventricular systole blood is flowing out of the other end of the arterial system through the capillaries into the venous system, and therefore that blood is flowing into the auricle. The contraction of the ventricles is therefore the cause of the dilating of the auricles, while the filling up of the auricles is the cause of the emptying of these cavities, and ultimately of the ventricles also. The action of the heart must, therefore, be of this intermittent character.

During the diastole, the repose of the heart, blood is flowing into its cavities; when an amount has accumulated sufficient to furnish the necessary stimulus to the contractility of the muscular substance, the contraction or systole takes place and blood is forced out; but as the circulatory system may be regarded as a closed tube, while venous blood

<sup>1</sup> Sitzber. d. Wiener Acad., 1855, Band xiv. S. 345

<sup>3</sup> London Medical Gazette, 1842, 2d ser. vol. ii. p. 561.

<sup>2</sup> Ibid., S. 373.

<sup>4</sup> Experimental Researches, 1853, p. 114.

is flowing into one end of the system the arterial blood will be flowing into the other or venous end. The intermittent flow of the blood, or the stimulus to the movements of the heart, further makes possible a far greater accumulation of the contractile force than if the stimulus were a continuous one. Were the heart to beat continuously, it would, like any other muscle, under similar circumstances, soon become exhausted, and indeed such is the case if the blood be retained indefinitely in any of the cavities of the heart. It is true that the part will, for some time, exhibit rhythmical movements, but, sooner or later, the movements will become infrequent, irregular, and finally cease altogether.

It is a matter of daily observation that the circulation, like the other functions, is influenced by the nervous system, but as the relation of the nervous system and the circulatory organs is quite a complex one, the consideration of this part of the subject will be for the present deferred.

In concluding our account of the heart it may be now appropriately mentioned, however, that while the action of the heart is greatly influenced by the nervous system, the heart itself is insensible. The insensibility of the heart is often observed in cases where it has been wounded, the patient being unconscious of pain, or, indeed, of any feeling at all. In the celebrated case of the Viscount Montgomery, so often mentioned by authors, and so well described by Harvey, the opportunity was offered of directly inspecting and feeling the heart. Harvey tells us, in the work<sup>1</sup> already referred to, that this individual was entirely unconscious of the application of his finger to the heart.

<sup>1</sup> Op. cit., p. 375.



## CHAPTER XX.

### THE ARTERIES.

WE have seen that at each ventricular systole the blood is forced from the heart into the pulmonary artery and aorta. The manner in which the venous blood passes through the pulmonary capillaries, and returns aërated arterial blood to the heart, will be described when the subject of respiration is considered, for the present let us follow the blood as it flows through the aorta and its branches, the arteries.

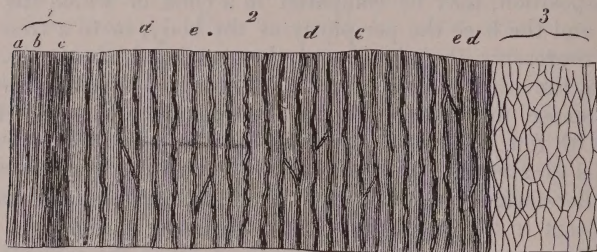
The arterial system, by means of which the blood is circulated to all parts of the body, consists of musculo-elastic tubes, which, in their general disposition, may be compared to a cone of which the heart is the apex, and the base the periphery of the body, or to a tree of which the aorta represents the trunk, and the arteries the branches. As we recede from the heart to the periphery the branches divide and subdivide, and anastomose, until, becoming microscopic, they pass into the capillaries. With few exceptions, the combined calibre of the branches of an artery is greater than that of the artery itself. There is a gradual increase, therefore, in the capacity of the arterial system as we pass from the heart to the capillaries. This increase of capacity, however, is not always as great as might be supposed, since the capacity of tubes are to each other as the squares of their diameters. For example, if an artery with a diameter of 4 cent. (1.6 in.) divides into two branches, each with a diameter of 3 cent., the difference between the capacity of the main trunk and its branches will be 2 cent. Thus,  $4^2$  equals 16,  $3^2 + 3^2$  equals  $9 + 9$  equals 18;  $18 - 16$  equals 2. As a general rule, the arteries run in nearly a straight course to the parts which they supply with blood. The branches gradually diminish in size, and comparatively few are given off between the main trunk and the capillaries. The aorta and the arteries, like the heart, are not nourished by the blood circulating in their cavities, but by blood from adjacent vessels, the arterial vasa vasorum, which have no direct connection with the arteries which they supply. The vasa vasorum, which include little veins, as well as arteries, are mostly restricted to the outer coat of the artery, but few penetrating the middle coat. The vasa vasorum of the arteries bear the same relation to the arteries that the coronary arteries and veins bear to the heart itself. The arteries are also supplied by nerves derived from both the cerebro-spinal and sympathetic systems, but principally from the latter. The manner in which these nerves modify the calibre of the arteries will be understood when their minute structure has been studied, to the consideration of which let us now turn.

The arteries, including the aorta, consist essentially of three coats (Fig. 152), an external fibrous, a middle elastic muscular, an internal epithelial. Each of these coats, however, can be shown to consist of

several subcoats, or layers, more or less developed, according to the size and situation of the artery.

The external or fibrous coat of the artery is mainly composed of fine bundles of white connective tissue, the filaments of which are usually disposed in a spiral manner around the vessel, and on the surface are often loosely adherent to surrounding parts: the inner surface of the fibrous coat, however, is intimately blended with the middle coat. Between the bundles of the connective tissue fibres, of which the external coat consists, are disposed in various amounts fine nets of elastic tissue; these nets are most abundant in the inner part of the external coat. To their internal coat the arteries owe chiefly their strength. The middle coat of the artery consists of layers of elastic and muscular tissue, which are disposed around the vessel in a circular manner. The relative amount of these tissues, however, varies according to the size and position of the vessel. In the largest arteries, those nearest the heart, the middle

FIG. 152.



Transverse section of the walls of the aorta, treated with acetic acid, and magnified. 1. Internal coat. *a*. Epithelium and basement membrane. *b*, *c*. Layers of elastic tissue. 2. Middle coat. *d*. Layers of elastic tissue. *e*. Muscular and connective tissue. 3. External coat, composed of fibrous tissue and fine nets of elastic tissue. (LEIDY.)

coat is composed mainly of elastic tissue, there being very little muscular tissue present, whereas, in the medium size arteries, the middle coat chiefly consists of muscular tissue, and in the smallest arteries of muscular tissue only. The muscular tissue is of the unstriated character, and consists of fusiform cells, or bands, with oval nuclei; they do not entirely surround the artery; the elastic tissue forms a more or less close network of fibres, which, from its membranous perforated character, is often known as the fenestrated membrane. A great deal of the elasticity, and all the contractility with which the arteries are endowed, are due to their middle coat.

The internal coat of the artery is essentially a continuation of the endocardium, or lining membrane of the heart, and consists of three layers, an outer elastic of the membranous fenestrated kind, a middle basement membrane, and an inner epithelial layer, composed of elongated lozenge-shaped cells. The outer elastic layer of the internal coat of the artery is intimately connected with the inner portion of the middle coat, while the basement membrane is that part of the artery which ultimately becomes the capillary. We have seen that the action of the heart is intermittent in character, each ventricular systole being followed by the diastole, a



period of repose during which no blood flows into the arterial system from the heart. If, however, a large artery near the heart be opened, it will be observed that the blood flows out of the artery continuously, both during the systole and diastole. With each ventricular systole, however, the jet becomes stronger; the flow in the artery, therefore, is not, like that in the heart, intermittent, but remittent. If the artery examined be situated, however, at a distance from the heart, near the periphery, the flow of the blood will be found to be but slightly remittent, indeed almost uniform, while finally, as we shall see in the capillaries, it is entirely so. The flow of the blood, then, as it passes from the heart through the arteries to the capillaries from being intermittent becomes remittent, and finally uniform. It is to the property of elasticity, with which we have seen arteries are endowed, that this transformation of an intermittent motion into a remittent one is due. For, during each ventricular systole, of the blood that is forced into the arteries a part only presses onward, the blood already in the arteries, the remaining part, presses outward the walls of the artery. From the moment, however, that the effect of the systole ceases—that is, during the diastole—through its elasticity the walls of the artery recoil on the blood which has distended them, and press it onward (the aortic valves preventing any regurgitation) immediately after the part of the blood that has just preceded—that is, the part forced forward during the systole. There are two successive waves of blood then in the artery, that of the systole and that of the diastole; they follow each other, however, so rapidly, that ultimately they merge into one, the movement of the blood in the capillaries becoming finally uniform. The elasticity of the artery favors, therefore, the onward movement of the blood.

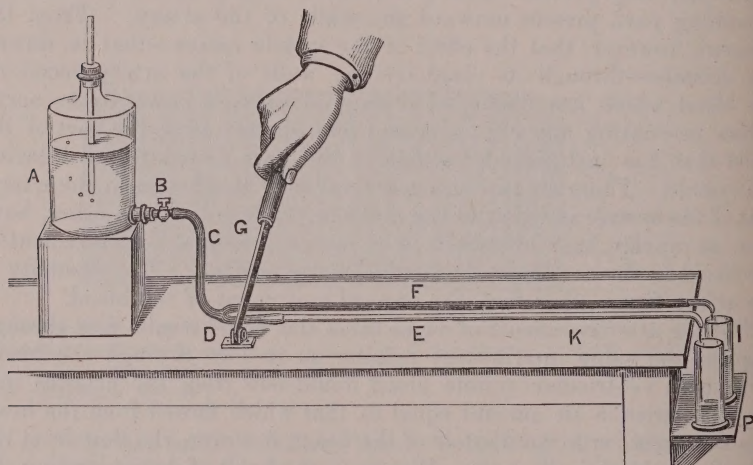
Did the arteries consist of rigid tubes the blood would flow through them in the same intermittent manner as it does through the heart. With each ventricular systole blood would flow from the arteries into the capillaries in an amount equal to that which flowed from the heart into the aorta, with the diastole of the heart, however, the flow from the arteries would entirely cease. We are in the habit of demonstrating the difference between the flow of liquids in elastic and rigid tubes by means of the apparatus described by Marey,<sup>1</sup> and which, slightly modified, is represented in Fig. 153. The apparatus consists of an elevated reservoir (A) holding about 20 litres (5 gallons) of water colored by aniline, and furnished with a stopcock (B) by means of which the supply of fluid can be regulated. To the stopcock, the orifice of which has a diameter of 1 cm. ( $\frac{2}{5}$ th of an inch), is connected a flexible, and, if possible, a non-elastic tube (C) about 70 cm. (28 inches) in length. The latter passes around a tin tube (D), which bifurcates so that the fluid from the reservoir can pass through the tube C into the tubes E and F simultaneously. One of these tubes consists of glass (E), the other of caoutchouc (F), the former (E) is connected with the tube D by caoutchouc. The two tubes (E F) have a length of 1.6 m. (5.12 feet) and a diameter of 1 cm. ( $\frac{2}{5}$ th of an inch). At their distal ends the tubes are bent downward so that the fluid flowing from them can

<sup>1</sup> Op. cit., 1881, p. 163.

be conveniently collected in the jars P I. The glass tube, as it terminates, is drawn out so as to simulate the capillary end of an artery, its orifice having a diameter of 2.5 mm. ( $\frac{1}{10}$ th of an inch). The same effect is accomplished, as regards the caoutchouc tube, by inserting into its distal end a tube of glass of the same length and diameter as that of the distal end of the glass tube. The tubes E F are supported by, and firmly bound to, the table K, which is painted white so that the colored fluid can be readily seen in the glass tube.

The reservoir being filled and the stopcock turned on, the colored fluid passes into the bifurcated tube and thence through the elevation and depression of the lever (G), worked by hand, in an intermittent manner, into the rigid glass tube and elastic caoutchouc one. The lever should be uniformly depressed and elevated at the rate of about sixty times to the minute and the fluid watched as it escapes from the tubes.

FIG. 153.



Apparatus to demonstrate the flow of a fluid through rigid and elastic tubes. (MAREY.)

It will be observed, from the reasons already given, that the flow from the rigid glass tube is absolutely intermittent, with each depression of the lever the flow entirely ceasing. On the other hand, the flow from the caoutchouc tube is distinctly remittent, the jet not ceasing but only diminishing with the depression of the lever and increasing again with its elevation. It is needless to add that the elevation and depression of the lever represent the opening and closing of the aortic valves, the escape of the fluid from the tubes the flow of blood through the constricted arteries toward the capillaries.

This experiment not only proves that the elasticity of a tube influences the character of the movement of the fluid flowing through it, but also of the quantity that escapes from it, for if the jars P I be examined it will be seen that the one collecting the liquid from the elastic tube is almost three times as full as that collecting from the rigid one. During an experiment lasting three minutes, while 2800 c. cm. (2.8



pints) of fluid flowed into the one jar, only 1000 c. cm. (1 pint) flowed into the other. This is as might have been expected when it is remembered that an elastic tube is capable of receiving more fluid than a rigid one, for two reasons: first, there is not only the quantity of fluid which, after entering the tube presses directly onward and which corresponds to the fluid in the rigid tube, but also an additional quantity which presses the walls of the elastic tube outwardly. It is this lateral fluid, so to speak, that follows and adds itself to the part which presses directly onward that converts the intermittent motion into the remittent one, and by just so much as the walls of the tube will give to this lateral pressure the amount of fluid entering the elastic tube will be in excess of that entering the rigid one. Second, it being remembered that the principal obstacle to the flow of a liquid through a tube is the friction of its walls, and that the friction is proportional to the square of the velocity of the current, it follows that as the effect of the dilatation of the artery is to diminish the velocity of the current through it, and therefore to diminish the amount of friction according to the square of the velocity of the current, the quantity of fluid delivered from the elastic tube will, therefore, be greater than that from the rigid one.

We have seen that the arteries are not only endowed with elasticity, but also with contractility or tonicity, as it was called by Bichat, and it has been shown, experimentally, by Poesseuille,<sup>1</sup> that the recoil of the walls of the artery upon the blood that had previously distended it is greater than can be accounted for by the elasticity of the artery alone. Indeed, the tendency of an artery is always to contract, to empty itself of its blood. For this reason difficulty is always experienced in injecting the vessels of an animal immediately after death.

If, during life, the calibre of the arteries is about equal to that observed after death, it is because the arteries are during life distended with blood.

That the arteries will contract independently of the elasticity or the recoil following upon the distention of its walls through the blood forced into the vessel by the heart, can be demonstrated by ligating an artery in two places and in a part of its course where no branches are given off, so as to exclude the influence of the general circulation, and then opening the artery at a point situated between the ligatures. Under such conditions, although the artery is uninfluenced by the action of the heart, etc., the blood will jet out with force and the artery will be almost completely emptied. When it is remembered, as we have seen, that in the smallest arteries the middle coat consists entirely of muscular fibres, there being no elastic tissue present, it becomes evident that the contractility, in such cases at least, must be due entirely to the action of the muscular fibres. Hence the distinction clearly made by John Hunter, that in the large arteries the recoil of the walls was due almost entirely to the elasticity; in the smallest arteries, on the contrary, to the contractility. The physiological significance of this distinction was also seen, Hunter attributing to the elasticity the conversion of the intermittent action of the heart into the remittent one of the artery, to the contractility the

<sup>1</sup> Journal de Magendie, t. ix. p. 44.

regulating of the calibre of the arteries, and, therefore, the supply of the blood to the system. Inasmuch as arteries therefore contract in virtue of their contractility as well as of their elasticity, and as after death the contractility disappears, as might be expected, the amount of contraction is greater in the living artery than the dead one. The contractility of the arteries can be easily demonstrated by the application of various stimuli, mechanical, chemical, electrical, exposure to air, application of cold, etc. Thus the mere scraping of the walls of an artery or the pricking of a needle will cause them to contract. Various chemical substances, such as sulphuric acid, ammonia, alum, and ergot, are among the most powerful stimuli to muscular contractility. Indeed, the usefulness of hæmostatics in arresting hemorrhage depends upon this property.

The smallest arteries readily contract under the influence of both the direct and indirect electrical currents. Simple exposure of the arteries to air suffices to produce a slow but permanent constriction of the vessel. The local application of cold—ice, for example—in stopping bleeding after wounds, is well known to the uneducated, the effect being due to contractility. The stimulus of great heat produces the same result.

We have already seen that, through nervous influence, the arteries contract. In speaking of the structure of the arteries, it was mentioned that the muscular fibres are supplied by nerves derived from the sympathetic and cerebro-spinal systems. The stimulation by electricity of these vasomotor nerves, as they are called, is followed by contraction of the arteries they supply, while division or paralysis of these nerves is followed by a dilatation of the vessels. The phenomena of blushing, of sudden pallor in the face, are familiar examples of the influence of the vasomotor nerves in modifying the amount of blood in a part; in the one case the vessels dilating, in the other contracting. When it is remembered that more blood is demanded by an organ at one time than another, a gland when secreting, for example, requiring more arterial blood than when quiescent, it becomes evident that there must be some means in the economy by which the amount of blood supplying any organ can be varied. It is through the vasomotor filaments that the nervous system modifies the calibre of the arteries, and, in that way, regulates the amount of blood distributed to different parts of the body. The origin and distribution of the vasomotor nerves will be considered in detail hereafter.

While it must be admitted that the contractility of the arteries favors somewhat the onward flow of the blood within them, without doubt the principal effect of their contractility is the regulation of the supply of blood through the modification of their calibre. It should be mentioned, as regards this contractility, that, by whatever means it is induced, whether the stimuli be mechanical, chemical, or electrical, ~~that~~ unlike ordinary striated muscle, it does not immediately follow the application of the stimulus, more or less time intervening, according to the stimulus used. It is also to be noticed that a temporary relaxation usually follows a contraction, and, if the stimulus be very intense, the contraction is followed by a dilatation, as if, for the moment, the contractility had been exhausted in producing its effect.



We have seen that during each ventricular systole the aorta and arteries generally become distended with the blood forced into them by the heart, and as the pressure of the blood is exerted both laterally and longitudinally, the artery must therefore enlarge in both these directions. The longitudinal enlargement of the artery is, however, so much more apparent than the transverse one, as will be explained presently, that the latter is usually masked or obscured. So much so, indeed, is this the case, that for a long time it was denied by physiologists that there was any transverse dilatation of the artery. While Harvey,<sup>1</sup> it is true, states that when an artery is divided, and held at the cut-end by the fingers, the dilatation is apparent, it must be admitted, however, that, to the ordinary eye, this is far from evident. The proof of the transverse dilatation of the artery, however, does not rest on the mere assertion of a physiologist, however celebrated, but can be readily demonstrated, either as shown by Flourens,<sup>2</sup> by placing around a living artery a watch-spring, the ends of which just meet during the relaxation of the vessel, and which separate during the lateral distention, or, by Poisseuille's<sup>3</sup> method, which consists in enclosing an artery in a living animal within a tube filled with water (the ends, of course, being closed), and the interior of which communicates with a capillary tube, serving as an indicator, in which the water rises or falls, according as the water is forced out of the tube by the lateral distention or transverse dilatation of the artery, or is sucked back again by the recoil of the wall of the vessel, due to its elasticity. The longitudinal expansion of the artery, or the elongation, is more easily demonstrated than the expansion in the transverse direction. As also shown by Flourens it is very evident, if the artery examined be slightly colored, and a needle as a guide be immovably placed on one side of the vessels with each ventricular systole and diastole the colored point on the artery will be observed to advance and recede in a longitudinal direction. The elongation of the artery is also very apparent in the vessels of the stump of an amputated extremity, and becomes quite evident in a vessel in which the blood flowing meets with an obstacle, as where the artery bifurcates, or runs in a tortuous course rather than a straight one. During the elongation of an artery the vessel frequently rises up out of its bed, experiencing considerable displacement; this is known as the locomotion of the artery, and is often seen in the temporal and radial arteries of old and emaciated persons.

On account of the extent of the vessel exposed during the elongation, the longitudinal expansion is far more evident than the transverse one, and, as we have already observed, quite obscures it. The increase of capacity due to the longitudinal expansion of the artery is, however, less than that due to the transverse one, for, as is well known, the capacity of the tube increases, as regards the length, in a simple ratio only, whereas, the capacity of tubes in the transverse direction increases not in a simple ratio, as the diameters, but as the squares of the diameters. For example, while a tube 51 cm. (20 inches) in length

<sup>1</sup> *Exercitatio altera ad J. Riolanum Opera Omnia*, 1756, p. 112.

<sup>2</sup> *Annales des Sciences Nat.*, 1837, t. vii. p. 106.

<sup>3</sup> *Op. cit.*, t. ix. p. 46

and 2.5 cm. (1 inch) in breadth, will contain about 290 c. cm. (0.2 pint),  
 a tube 51.5 cm. (20.5 inches) in breadth, will contain 292 c. cm., or  
 only 2 cm. more, thus:

$$51 : 51.5 :: 290 : x \text{ equals } 292;$$

whereas, a tube 51 cm. long, but 2.8 cm. (1 inch) in breadth, will contain 360, thus:

6.25, or  $(2.5)^2 : 7.84$ , or  $(2.8)^2 :: 290 : x$  equals 360, or nearly 70 c. cm. more than the tube 51.5 cm. long, but only 2.5 cm. in breadth—350–292 equals 68.

The elongation and transverse dilatation of the arteries due to the distention of their walls by the blood forced into them by the heart at each ventricular systole constitute the pulse. It will be observed that the pulse, or the expansion of the artery, is synchronous with the contraction of the ventricle of the heart, not with the heart's expansion, as was thought by Galen, and the ancients generally. Although this truth seems to have been known to a writer who lived during the early part of our era, it remained for Harvey to demonstrate it in modern times. Ordinarily, neither the elongation nor transverse dilatation of an artery or its pulse is visible to the naked eye, or appreciable even by touch alone. It is for this reason that the observer presses with his finger more or less the artery examined, thereby constricting the vessel and so increasing the velocity of the blood, it flowing faster as the artery becomes smaller, the same amount of blood passing through in a given time; this, as we have seen, increases friction, and so causes an obstacle to the flow, which, within limits, increases the force of the heart, and, therefore, the distention of the artery, and so makes the beating of the vessel or the pulse more apparent.



## CHAPTER XXI.

### THE ARTERIES.—(*Continued.*)

#### SPHYGMOGRAPH, ARTERIAL SCHEMA.

No artery in man can be directly measured, either as regards its expansion or its pressure. In feeling the pulse, however, the endeavor is made to measure both by the sense of touch alone.

While the experience of every physician shows to what an extent slight variations in the pulse can be appreciated by the tactus eruditus alone, nevertheless it is only by means of the graphic method that the conditions on which the production of the pulse and its variations depend can be successfully investigated. By the graphic method, as we have seen, a pictorial representation, a trace of some kind of the phenomena occurring can be obtained and preserved, by means of which slight variations, due to change of conditions, become at once evident that would be entirely unappreciable by the eye or touch unaided, and ~~that~~ by a comparison of the traces obtained from the examination of the living artery with those obtained from a tube corresponding to an artery in an artificial apparatus representing the general vascular system, the manner in which the pulse is produced, and the conditions on which its variations depend, can be demonstrated.

The advantage of such an experimental investigation of the pulse, the practical application that can be made of it in investigating the cause of disease, will be at once appreciated after the sphygmograph and the arterial schema, the apparatus we use in studying the pulse, have been described, and the results obtained by them shown.

The object of the sphygmograph (sphygmos, a trace, and grapho, to write) is to measure the succession of the alternate dilatations and contractions of an artery due to the blood forced into it by the beating heart, to magnify these movements, and to register them on a surface moving at a uniform rate by clock-work. The arterial schema, or artificial artery is an apparatus representing the general vascular system by means of which we can produce an experimental pulse, and from it, by means of the sphygmograph, obtain a trace, which can be compared with that obtained by the sphygmograph from the natural pulse. By such a comparison it will be observed that the trace made by the pulsation of the artificial artery, differs from that made by the living one only in degree, not in kind; the natural inference is, therefore, that the cause of both traces must be essentially the same. Further, by slightly changing the action of the arterial schema, traces can be produced which so closely simulate those obtained from the living pulse in various diseases that there can be but little doubt that the cause of both is the same.





the brass bar N, carrying the knife-edge D, the latter, in turn, elevating the registering lever A, of which one end (C) is supported by a horizontal rod passing through it and connecting the sides of the brass frame, while the other movable end (A) terminates in a metal joint, which registers the motion of the pulsation on a piece of paper (Fig. 155) blackened by passing it to and fro through the flame of a kerosene lamp. The paper is fastened to a copper plate, which is moved at a uniform rate by the clock-work (Fig. 155). As the distance between the supporting rod C and the knife-edge D is much less than the length of the lever, the vibrations of the extremity of the lever (A) are far more extensive than the vertical movement of the spring I and screw T. By means of the screw T the distance between the steel spring I and the registering lever A can be varied at will without interfering with the mechanism by which the movement is transmitted. The distance between the brass frame and the ebonite surface can also be increased or diminished, according to the direction in which the screw Y is turned, and, in this way, the pressure on the artery may be varied; the variation in the pressure is measured by the scale (Fig. 156), which has been experimentally graduated by turning the instrument upside down, and successively placing a series of weights on what would be ordinarily the lower surface of the spring, but which is now the upper surface, and observing the extent of its deflection and marking the scale correspondingly. Finally, by means of a movable clamp, there can be adapted to the sphygmograph, when desirable, a delicate tympanum, with registering lever, in connection with a cardiograph, so that the traces of the cardiac and arterial pulsation can be registered simultaneously on the blackened surface.

To take a trace with the sphygmograph of the radial artery, which is the vessel usually examined, the forearm should be supported on something, a table, for example, the back of the wrist resting on a cushion or padding, so that the dorsal surface of the hand will be inclined, with reference to the forearm, at an angle of 20 to 30 degrees. The instrument must be so placed on the wrist that the block rests upon the trapezium and scaphoid, while the extremity of the spring is opposite the styloid process of the radius, the general direction of the sphygmograph will then be parallel with that of the radius. In making an observation it is best to begin by adjusting the instrument so that the ivory button on the under surface of the spring is at such a distance from the bone that the artery is pressed upon during its entire expansion, and yet not so compressed as to obliterate at any moment its cavity.

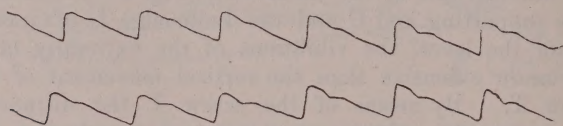
To those unfamiliar with the use of the sphygmograph, perhaps it will be well to begin by arranging the spring so that it will exert a pressure sufficient to flatten the artery against the radius and then to diminish the pressure until the effects of such compression disappear, and thus to take traces of the maximum and minimum pressures, and one then of an intermediate character.

Having described the sphygmograph and the manner of using it, the following figures will illustrate the character of the traces taken by it. Thus, for example, Figs. 157, 158, and 159 are obtained from the

radial and femoral arteries in a healthy man of about thirty years of age. Figs. 160 and 161 are from the radial of a woman *æt.* sixty-five and of a man *æt.* seventy respectively, in both of which cases the arteries were in an atheromatous condition.

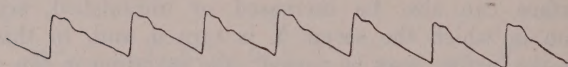
Let us now consider the arterial schema and the manner in which the artificial pulse is produced, and then compare the tracing of such a pulse

FIG. 157.



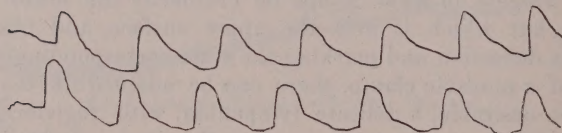
Sphygmographic tracing from radial artery of a man *æt.* twenty-five.

FIG. 158.



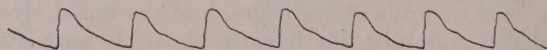
Sphygmographic tracing from radial artery of a man *æt.* thirty.

FIG. 159.



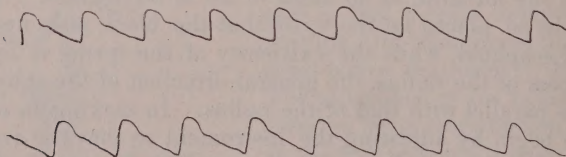
Sphygmographic tracing from femoral artery of a man *æt.* thirty. (A. P. B.)

FIG. 160.



Sphygmographic tracing from radial artery of a woman *æt.* sixty-five. Atheromatous arteries.

FIG. 161.



Sphygmographic tracing from radial artery of a man *æt.* seventy. Atheromatous arteries.

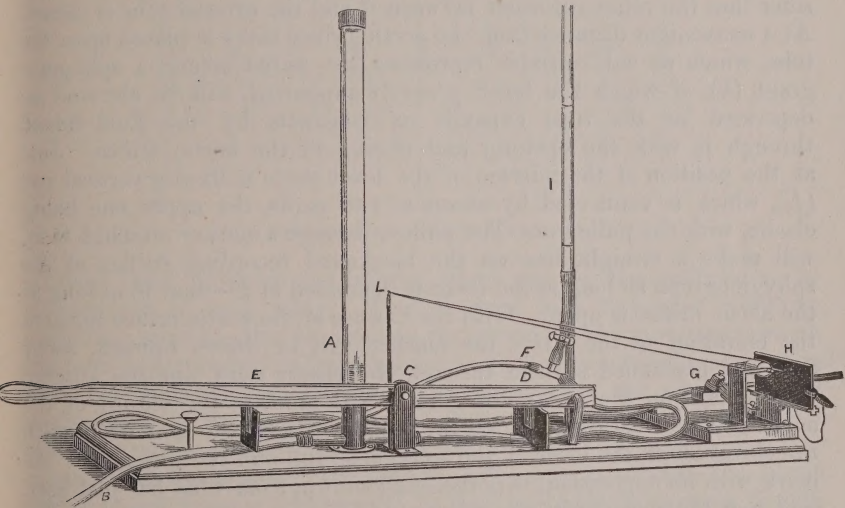
with those just exhibited. There are several different kinds of arterial schema, from the simple one of Weber to the elaborate apparatus of Marey, that are used in studying the phenomena of the circulation. For our present purpose the instrument (Fig. 162) described by Sanderson<sup>1</sup> and constructed for the author by Hawksley, will suffice. It is true that the apparatus does not resemble in form at all the heart, aorta, etc., but as the object of the arterial schema is not meant to illustrate the structure of the parts but their action, this is a matter of no moment.

<sup>1</sup> Handbook Phys. Lab., p. 230. Phila., 1873.



It consists essentially of a reservoir supplying the colored water representing blood, which should stand at a height of from 2 to 3 metres (6 to 9 feet), of an elastic tube (*B D C*, etc.) several metres long, representing the left side of the heart, aorta, arterial system, etc., of a lever (*C*) 53 cm. (21 in.) in length and which is so arranged that, as it is depressed at the end nearest *D*, it closes the elastic tube at *D* and opens it at *E*, and when elevated opens the tube at *D* and closes it at *E*. This alternate closing and opening of the tube at *E* and *D* imitate the action of

FIG. 162.



Schema for demonstrating the nature of the arterial movements. *A*. Glass tube which represents the heart. *B*. The tube by which *A* communicates with a cistern at a height of ten or twelve feet above it (*A* much smaller head of water is sufficient.) *C*. The lever by which the two valves *E* and *D* are worked, the same act which shuts the one opening the other. *F*. Commencement of the experiment tube, which is of black vulcanite. At *F* the tube communicates with a long vertical tube of glass, only part of which is seen; it is closed at the top, and usually shut off from *F* by a pinchcock. At *G* the tube passes under the spring of the sphygmograph, the frame of which rests on a block (below *G*). By error, the tube has been drawn on the wrong side of the block. *H*. The blackened plate of the sphygmograph. To the left of it is seen the cylinder, with its needle for recording the time which intervenes between the opening and closing of the aortic valve, *L*. A rod which is firmly fixed in the lever, and is connected by two cords, one of which is elastic with the cylinder. (SANDERSON.)

the mitral and aortic valves by means of the spring at *G*; when the apparatus is not working the aortic orifice is kept closed. The portion of the tube lying between *D* and *E*, which represents, therefore, the left ventricle, is 30 cm. (12 in.) in length, communicates with the vertical glass tube (*A*) 54 cm. (21 in.) high and with a diameter of 9 cm. (3.5 in.); this tube can be opened or closed at its upper end by a stop-cock. When the lever is elevated and the tube opened at *E*, or the mitral orifice, the colored fluid from the reservoir flows up into the tube *A* compressing the air within it, according to Mariotte's law, the volume of air diminishing as the pressure increases; when the lever is depressed and the tube open at *D*, or the aortic orifice, the compressed

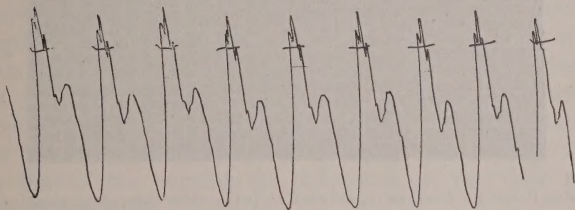
air in the tube *A* suddenly expands and forces the water into the tube beyond (*D*), which, of course, corresponds to the aorta. The expansion of the air then represents the force of the contracting heart. At a distance of 15 cm. (6 in.) from the aortic orifice the elastic tube communicates through a T-shaped connecting tube on the one hand, with a long vertical glass tube (*I*), and on the other with the tube *F*, which, gradually becoming smaller and then larger again, represents the arteries, capillaries, and veins. The communication between the tube *F* and the tube *I* can be opened or closed by means of a pinchcock. The use of the tube *I* will be explained presently. For the moment we will consider that the communication between it and the arterial tube is closed. At a convenient distance from the aortic orifice there is placed upon the tube, which we will consider represents the radial artery, a sphygmograph (*h*), of which the lever, properly supported, will be elevated or depressed as the tube expands or contracts by the fluid forced through it with the opening and closing of the aortic orifice. Just at the position of the fulcrum of the lever there is fixed a vertical rod (*L*), which is connected by means of two cords, the upper one being elastic, with the pulley *m*. The pulley, through a marker attached to it, will make a straight line on the blackened recording surface of the sphygmograph as long as the lever is depressed at *E*—that is, as long as the aortic orifice is open. With the closure of the aortic orifice through the elevation of the lever, the marker will be drawn upward, away from the blackened surface, through the elastic cord, and the absence of the mark on the blackened surface will indicate the closure of the aortic orifice. As the mark on the recording surface is coincident with the elevation of the lever of the sphygmograph and the absence of the mark with its depression, it is therefore shown, from what has just been said, that the elevation of the sphygmograph lever is coincident with the opening of the aortic orifice, and, therefore, with the ventricular systole, while the depression of the lever is coincident with the diastole.

*Fig. 162* | The construction of the apparatus being now understood, let the sphygmographic trace Fig. 161, taken by it, be compared with that of Fig. 157, representing the sphygmographic trace of the natural pulse. By such a comparison it will be observed that the difference between the traces of the natural pulse and that of the schema is one of degree rather than of kind. In both traces we have seen the same movements succeeding each other in the same order. With the expansion of the artery we have the elevation of the lever with the contraction, the descent, then the secondary rise or diastole, and finally the descent again. As in the case of the natural heart so in that of the schema, it is seen that as the aortic valve (*D*) is opened the artery expands, the lever rising and the vessel remains full as long as the artificial heart is acting, that with the cessation of the flow of liquid from behind the artery contracts, the lever descending. That the ascent and descent of the lever are due to the cause just assigned can be shown by the motion of the marker attached to the pulley *m* in the manner explained above. As long as the aortic orifice *D* is open the marker remains in contact with the recording surface of the sphygmograph, but with the closure of the aortic orifice the marker is pulled away. The trace (Fig. 161), as recorded,



exhibits then a line broken at regular intervals. When this is compared with the sphygmographic trace of the artery it will be observed that there is an exact correspondence between the time during which the heart is acting and the time elapsing between the beginning of the expansion and the commencement of the contraction, the expansion evidently, therefore, depends upon the contraction of the heart. By a careful examination of the traces produced by the arterial schema it can be seen also that the forcing of liquid into the arterial tube by the

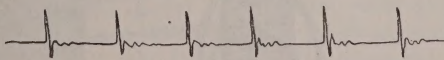
FIG. 163.



Tracing obtained with arterial schema.

artificial heart produces two effects, which can be demonstrated to be independent of each other. One of these is a molecular vibratory oscillating motion—that is, a to and fro pendulum-like movement, which has been appropriately called, from its mode of producing the percussion wave, the other the transmission of the pressure of the artificial heart at the moment the aortic orifice is open to the liquid in the arterial tube, and which is known as the pressure-wave. To produce the percussion wave by means of the schema, one has only to close the aortic orifice *D* and arrange the lever *C*, so that by suddenly rapping it with a hammer a percussion shock can be imparted to the tube beneath. The trace of the percussion wave produced in this way (Fig. 164) shows that the sphygmographic lever is jerked up the initial ascent, the descent being extremely abrupt. In order to obtain a trace of the

FIG. 164.

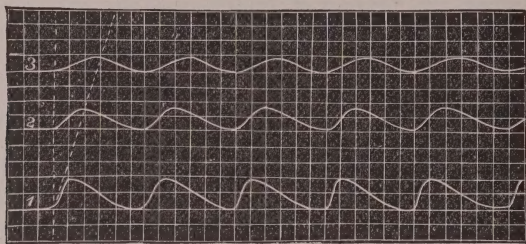


Tracing of percussion wave obtained with arterial schema.

pressure wave, which is also a vibratory motion (Fig. 165), it is best to use an elastic bag (Fig. 166, *B*), which communicates, on the one hand, with a reservoir of water and on the other with a long elastic T-tube, to which are adapted at intervals three tambours with levers (*l l' l''*) recording upon the same cylinder, or the tube can be placed under three levers provided with tambours (one of which is represented in Fig. 167), the latter being connected by tubing with the tambours of the secondary levers. The bag should be of a size that it can be squeezed by the hand. The object of having three such sphygmographic arrangements is to obtain traces at different distances from the heart, the source of the pressure, as well as to demonstrate the postponement of the pulse, which

will be shown immediately. Inasmuch as the action of the squeezing hand is very unlike that of the contracting heart, the hand contracting gradually and weakly relatively to the resistance, the heart, on the other hand, contracting suddenly and most powerfully at the beginning of its action as might be expected, the traces of the pressure wave, like that of

FIG. 165.

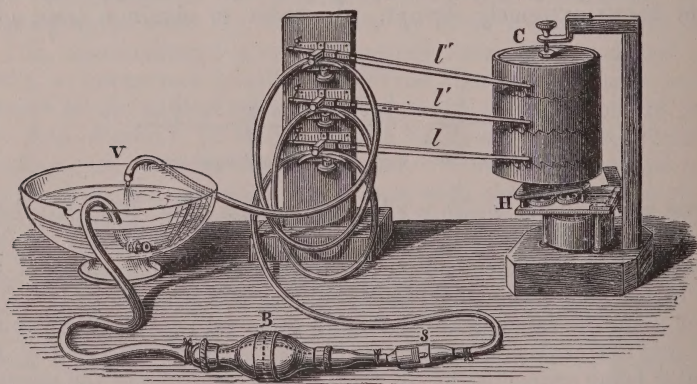


Tracings showing the contractions and expansion of an India-rubber tube, along which water is propelled in an intermitting stream by squeezing with the hand, at regular intervals of time, an elastic bag provided with valves, with which the tube is in communication; the bag thus represents the heart. The three tracings are drawn simultaneously, and exhibit the expansive movements of the tube at three different distances from the bag, the upper tracing being taken at the greatest distance. (SANDERSON.)

the percussion wave, will be entirely different from the trace of the natural pulse or that produced by the arterial schema.

It will be seen by examining the traces of the pressure wave (Fig. 165) that the lever does not descend as abruptly as in the case of the percussion wave, as the recoil of the arterial wall due to its elasticity is not instantaneous, hence the lever will momentarily remain at the height to which it has been elevated, and this period will be prolonged in proportion as the elasticity of the artery is diminished; hence, in old

FIG. 166.



persons; in whom the arteries are not very elastic, the curve at the summit is rounded off and the descent is a gradual one. It will be also noticed that the expansion in the distal part of the tube (the upper of the three traces) culminates later than in the proximal part.



In the traces obtained from the natural pulse, or from that of the arterial schema, we see the effects of both the percussion and pressure waves: the abrupt line of ascent is due to the percussion wave the temporary elevation of the lever being due to the recoil not at once following the distention due to the pressure wave. As a general rule, in the natural pulse both these effects follow each other very quickly, and are merged into one another. As we shall see, however, in a moment, under certain circumstances one may be far more evident than the other. Did the natural pulse consist of the percussion wave only, it would be felt at the same time in all parts of the system, as the percussion wave is practically transmitted instantaneously through tubes of the length of the arteries. Any one can readily convince himself, however, in his own person, that there is a gradual retardation of the pulse from the heart to the periphery, by feeling the left carotid artery with the thumb and index finger of the left hand, and the left radial with those of the right. The beat of the radial artery will be felt later than that of the carotid, the difference in the time of the beat being quite appreciable.

This postponement of the pulse is due to the fact that the pressure wave is transmitted at a slower rate of vibration than the percussion wave, and the reason is obvious. At the moment that the blood bursts out of the contracting heart into the aorta, the wall of the vessel yields to the pressure and expands during the relaxation of the heart, the walls of the artery through its elasticity recoil upon the blood and add pressure to the heart pressure which has just preceded it. This expansion, however, as we have seen, begins at the proximal end of the artery and is transmitted in a wave-like manner to the distal end necessarily, therefore the expansion, or the pulse, will be felt later in the distal than in the proximal end of the artery. Were the artery rigid instead of elastic, there would be no postponement, and if tense at the moment of the ventricular systole, little or none.

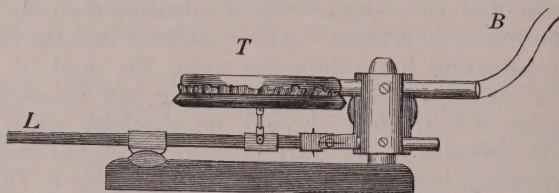
It was shown by Weber that the pulse wave (pressure wave) is transmitted at a rate of about 9 metres (28 feet) a second. Weber<sup>1</sup> determined this velocity by observing with chronometers the difference in time of the beat of the facial and dorsalis pedis arteries, measuring the distance of the facial artery from the heart as accurately as possible, and the distance of the dorsalis pedis from the facial, and subtracting the first distance from the second, the difference of distance the pulse wave passed over in the second case as compared with the first will account for the difference in the time of the beats, and give approximately the distance passed over by the pulse wave in one second. Supposing that the ventricular systole lasted four-tenths of a second, the pulse wave would be 3.6 metres (11 feet) long ( $9 \times \frac{4}{10} = 3.6$ ), and there would be two and a half waves in a second ( $\frac{9}{3.6} = 2.5$ ), consequently the anterior end of a pulse wave would have reached the extremities before the posterior end had left the left ventricle. It would appear, however, that this estimate of the length of the pulse wave is somewhat exaggerated, Czermak<sup>2</sup> having shown by the photo-

<sup>1</sup> Muller's Archiv, 1851, S. 537.

<sup>2</sup> Carpenter's Physiology, p. 316.

sphygmograph that the pulse wave is about 1.5 metres (5 feet) long, requiring about one-sixth of a second to pass from the heart to the foot. In speaking of the velocity of the pulse wave, of course it is to be understood that this has no reference to the velocity with which the mass of blood flows from the heart to the periphery. The latter motion is one of translation, and, as we shall see, is slower than the former or the pulse wave, which is molecular and vibratory in character. Weber<sup>1</sup> well says "*Unda non est materia progrediens sed forma materiae progrediens.*" "The gradual retardation of the pulse is well shown in the traces (Fig. 165) taken by means of the apparatus already described (Fig. 166). By adapting to the recording cylinder the marker of a chronographic apparatus, the exact difference in the time of the beats of the proximal and distal parts of the tube can be determined. The fact of the pulse consisting of two kinds of vibratory movements, the percussion and pressure waves differing as regards their velocity, explains why the pulse appears in some persons to be quickened, while in others to be postponed. In certain individuals the pressure wave is

FIG. 167.



Lever, etc., for receiving pressure wave. L. Lever. T. Tambour. B. Tube conducting to recording tambour.

instantaneously transmitted, is most felt, and the pulse seems quickened; in other cases the pressure wave is more slowly transmitted, is most sensible to the touch, and the pulse seems delayed. By examining the sphygmographic traces of the natural and artificial pulse it will be observed, as has been already mentioned, that the lever descends for a short distance, then slightly rises again, descends to the level from which it was first elevated; in some cases even the lever rises a third or a fourth time before finally descending. This secondary elevation of the lever is known as the dicrotic pulse, and is caused essentially by the return of the pulse wave from the capillaries back toward the heart.

We have just seen that the pulse wave is retarded, the arteries near the heart therefore expand before those near the periphery; while the expansion is subsiding in the smallest ones it is beginning in the large arteries, so that there is a moment when the pressure is greater in the latter than in the former, the aortic valves being closed behind, and the capillaries offering resistance in front, the only way in which equilibrium can be restored is by increase of pressure toward the heart with diminution at the periphery. As regards the cause of the dicrotic pulse, the only question about which there still appears to be any doubt among

<sup>1</sup> Marey, op. cit., p. 227.



physiologists is, whether the aortic valves are opened or closed during its production, and whether the secondary pulse wave, to which it is due, is a centripetal or centrifugal one—that is, whether the pulse wave as it returns from the capillaries toward the heart elevates the lever the second time, or whether it passes first back to the aortic valves, and after it is reflected back toward the capillaries then elevates the lever. The result of experiments with the schema would lead us to conclude that in some cases the dicrotic pulse is due to the return of the pulse wave from the capillaries, while in others it is caused by a secondary recoil from the aortic valves, and that when there is a tertiary as well as a secondary elevation of the lever the former is due to the aortic, the latter to the capillary rebound. It will be remembered that, in describing the arterial schema, it was stated that the main tube bifurcated at *F*, one end continuing as the main arterial tube, while the other could be closed or adapted to a vertical glass tube (*I*). This tube, which is about 01.1 metre (4 feet) high and 1 cm. ( $\frac{2}{5}$ th of an inch) wide, is closed at the top, and serves, through the rise and fall of the level of the fluid it contains, as an indicator of the state of the equilibrium of the fluid in the main tube. With the opening and closing of the aortic valves the level of the fluid in the tube will rise and fall, and if there be any dicrotism present it will be indicated by a secondary rise of the level of the fluid in the tube, and the phenomena of the dicrotic pulse in this way made quite evident. Now, if there be placed upon the main tube or artery a sphygmograph, as before, and also a second sphygmograph about 01.1 metre (4 feet) from the first one, and the main tube, about the same distance from the second sphygmograph, be somewhat constricted to represent the capillary resistance, it will be observed that, as the aortic orifice is open, the level of the fluid in the vertical glass tube rises; that the levers of the sphygmographs are successively elevated, the second one a fraction of a second later than the first; that the elevation of the fluid and the levers is succeeded by a depression, and is followed by a secondary elevation of the fluid and of the levers, the level of the fluid and the levers finally descending again to the level from which they were first elevated. If, during this experiment, the levers of the sphygmographs be carefully watched, it will be observed, as was just mentioned, that as the aortic valve is opened—that is, as the pulse wave passes from the heart toward the capillaries, the elevation of the lever of the proximal sphygmograph takes place sooner than that of the distal one, the pulse wave being retarded; whereas, during the production of the dicrotic pulse it is the lever of the distal sphygmograph that is elevated first, showing that the dicrotic elevation is due to the return of the wave from the capillaries toward the heart, and that the dicrotism occurs at a distance of more than a metre (4 feet) from the aortic orifice as the wave is passing toward the heart. On the other hand, if the levers are elevated for the third time, then it is the lever of the proximal sphygmograph that is elevated first, showing that the tertiary elevation of the lever, like the primary, is due to a pulse wave flowing from the heart to the periphery. The dicrotic pulse can be produced with the schema, whether the main tube be constricted at some distance from the sphygmograph or at its point of application, and whether the aortic orifice be open or shut; in

the latter case the aortic valve offers a resistance, in the former the column of liquid.

According to Marey,<sup>1</sup> if the aortic valves be destroyed there is no dirotic pulse. This is as might be expected, as under such circumstances there would be little resistance offered to the return pulse wave, and therefore little dirotic distention. The dirotic pulse appears, therefore, to be due to secondary pulse waves, in some cases transmitted in a centripetal, in others in a centrifugal direction. The amount and exact cause of the dirotic pulse must therefore vary with the general condition of the vascular system. In health, for example, when the vessels are tense it is seen only as a slight interruption in the descent of the lever. In fever, on the other hand, when the vessels are distensible, it is so marked that the pulse feels as if it were double.

When it is remembered that, as the blood is propelled forward into the arterial system, it is being continually diverted laterally through the distensibility of the walls of the arteries, and that as the quantity of blood forced forward at each ventricular systole is limited in quantity, it must follow, as we recede from the heart to the periphery, that there will be less and less blood forced forward. The blood having been progressively absorbed, so to speak, by these lateral distentions in the proximal portion of the arteries, there will be less, therefore, to distend the distal parts. The pulse being due to this distention, must, therefore, be weaker in the arteries at a distance from the heart than in those near it, and must ultimately disappear in the smallest arterioles altogether. As a fact, the pulse is rarely felt in arteries having a diameter less than  $\frac{1}{3}$  of a mm. ( $\frac{1}{75}$ th of an inch). It is for this reason that in the case of an aneurism, the lateral distention being here greatly exaggerated, that the pulse is often absent in that portion of the artery situated beyond the seat of the disease. In the case of aneurism of the aorta, the pulse may be absent in all of the arteries of the body.

While the description of the pulse in disease belongs rather to works on medicine and therapeutics, it may not appear superfluous to mention that pathology confirms the views that have just been offered as to the production of the natural pulse. Thus, in an ossified artery, there is no pulse, because dilatation is impossible. When the arteries near the heart are rigid, the pulse is jerky, and the flow of blood is intermittent, not remittent. We see the same kind of pulse when the walls of the arteries are relaxed, unable to recoil thoroughly on their contents. If the artery be irritable, and at the same time distensible, the pulse will be exaggerated, and can be seen by the naked eye when, otherwise, it is usually imperceptible. The character of the pulse is profoundly affected by the conditions of the system, modified by general disease. Thus the large compressible pulse of fever, the hard pulse of Bright's disease, the small pulse of peritonitis, the soft pulse of collapse, etc., are well known to the physician.

Finally, it has been shown by Vierordt and Aberle<sup>2</sup> that there is a daily variation in the calibre of the arteries that must influence somewhat the character of the pulse, the radial artery, for example, being larger in the evening than in the morning.

<sup>1</sup> Op. cit., p. 255.

<sup>2</sup> Archiv f. physiol. Heilkunde, 1856, B. xv. S. 574.



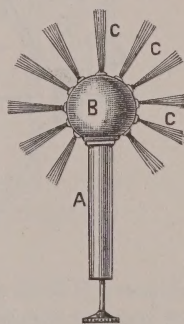
## CHAPTER XXII.

### PRESSURE AND VELOCITY OF THE BLOOD IN THE ARTERIES.

By blood pressure, whether it be cardiac or arterial, etc., is meant the pressure or force that is exerted by the blood upon the surface of the vessel containing it, or, what is the same thing, the force that is required to be put forth by the walls of the vessels in order to sustain the column of blood within them. Before showing the manner in which the blood pressure is determined in a living animal, let us first endeavor, however, to illustrate, by a few simple experiments, the manner in which the pressure of liquids in general is determined.

It is well known, as first shown by the distinguished geometrician Pascal, that the pressure exerted anywhere upon a mass of liquid, assuming the latter to be perfectly fluid and uninfluenced by gravity, is transmitted undiminished in all directions, acting with the same force on all equal surfaces, and in a direction at right angles to those surfaces. That the force exerted upon the mass of a liquid is transmitted in all directions, and at right angles can be readily shown by means of the apparatus represented in Fig. 168. This consists of a cylinder provided with a piston, fitting into a hollow sphere pierced with numerous holes, into which are fitted small cylindrical jets placed perpendicularly to the sides. The sphere and cylinder being filled with water, and the piston depressed, the water will be observed to spout out from all of the jets, and not simply from the one opposite the piston. In order to show that the pressure is transmitted, not only in all directions, but equally, we make use of an apparatus very similar to the one just described, and represented in Fig. 169, it differing only in that the perpendicular jets projecting from the sphere contain closely fitting, but easily movable pistons, each piston having the same area. The sphere being filled with water, the latter, by virtue of its weight, will press equally upon the surface of all the pistons. Neglecting the influence exerted by the weight of the water, and the friction of the pistons, it will be observed that if a given pressure ( $P$ ) be exerted upon the piston  $A$  the water will transmit the same pressure to the other pistons ( $B\ C\ D$ ), which will move outwardly, unless they are each subjected to an equal and opposite pressure ( $P$ ). It is evident, therefore, that the pressure ( $P$ ) exerted upon  $A$  is not only transmitted in a straight line upon  $B$ , but equally upon  $C$  and  $D$ —that is, equally in all directions. If now the axes of the jets  $B\ C\ D$  be disposed parallel to each other, and made to approach until they form one, and

FIG. 168.



Apparatus to demonstrate the equality of pressure in all directions.

for the three pistons a single one be substituted, as in Fig. 170, the conditions of the pressure are in nowise changed, but it becomes at once evident that the pressure exerted upon the piston A, and transmitted by the fluid, is proportional to both the number and area of the pistons, whether existing separately as B, C, and D, or combined as B C D. That is to say, if a weight of one pound be placed upon the piston A, the three pistons B, C, D, or the one piston B C D, will be pressed outward by the pressure transmitted through the liquid, unless a weight of one pound be placed upon each of the pistons B, C, D, or of three pounds upon the piston B C D. Suppose, however, that the apparatus be constructed of the form represented in Fig. 171, in which, as before,

FIG. 169.

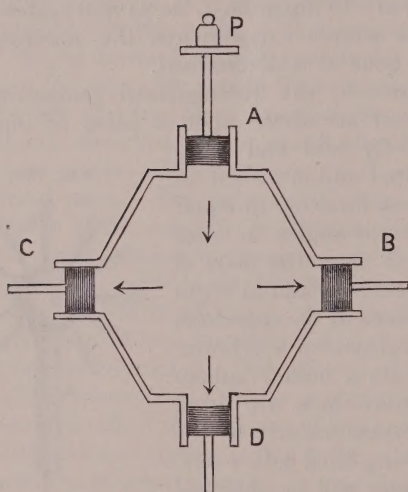
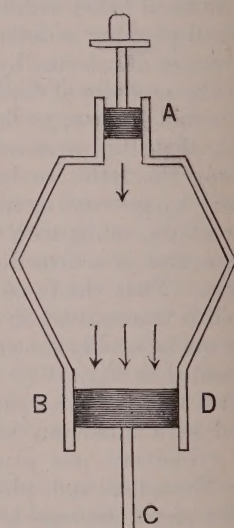


FIG. 170.



the large piston A has three times the area of the small one B, and carries three times as heavy a weight, it will be observed that while the small piston B with a weight of one pound and an area of one inch, descends through three inches, the large piston A, with an area of three inches, and with a weight of three pounds, ascends through only one inch, equilibrium being then established, just as a lever whose arms have a length respectively of three and one inches will be balanced by suspending a one pound weight at the end of the long arm, and a three pound weight at the end of the short one. It is perfectly evident that in neither case is there any absolute gain of power, for what is gained in weight is lost in height or distance.

In practical mechanics the Bramah press is a beautiful application of the principle just enunciated, in which a pressure of 300 pounds exerted upon a piston corresponding to A will exert a pressure of 30,000 pounds upon a piston B C D, supposing the sectional area of the latter to be 100 times that of the former. It must not be forgotten,

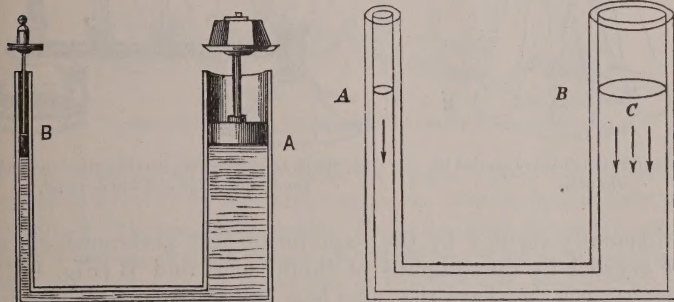


however, that in the Bramah press, as in the simple apparatus just described, and in the case of the lever with unequal arms, that the greater weight is elevated only a fractional part of the distance through which the lesser weight has descended, and that what is, therefore, gained in weight is lost in distance. The significance of this important truth in the study of blood pressure will very soon become evident.

Now, on reflection, it will become evident from what has just been said with reference to the transmission of pressure through fluids, that the pressure exerted by the particles of water against each other must be estimated in exactly the same manner as we have estimated the pressure  $P$  transmitted to the base of the pistons (Fig. 171), or, what is the same thing, to the walls of the vessel containing the water. It follows, therefore, that if the weights and pistons be removed from the apparatus (Fig. 171), that the water will rise to the same level in both of its limbs (Fig. 172), proving that the pressure exerted by the water in  $A$  and  $B$

FIG. 171.

FIG. 172.

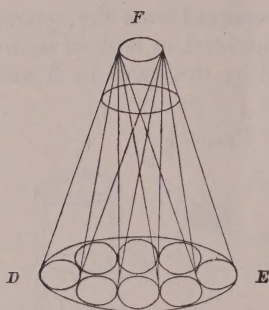


Principle of the hydraulic press.

must be equal and opposite, notwithstanding that the limb  $B$  contains three times as much water as the limb  $A$ , for if the pressure exerted by the water in  $B$  were greater than that in  $A$  the level of the water would rise higher in the latter than in the former. It follows, therefore, from the principle of Pascal, or the equality of pressures, that the pressure exerted by a fluid is independent of the quantity of the fluid, and of the form of the vessel containing it, but is dependent for the same fluid on the area of the base upon which the pressure is exerted, and the height of the column of liquid above it. For let us suppose that the vessel, whose liquid contents press upon the bottom, be of a tapering form, such as is represented in Fig. 173, and that the bottom  $D E$  be divided into eight areas of the size, as that of the mouth  $F$ . From what has been said of the pressure being transmitted equally in all directions, it follows that the weight of a small liquid layer, say half an inch thick at the top, will be transmitted undiminished to the eight areas of the bottom, producing the same pressure as if eight of such layers of liquid were separately placed upon them. In the same manner, a layer half an inch thick, but situated as much lower down in the liquid, so as to have twice the area of  $F$ , will produce the same pressure upon the

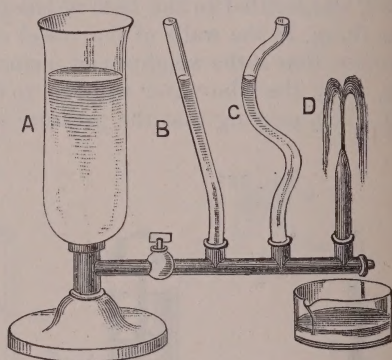
bottom as if four such liquid layers were laid there—that is, the same as the pressure due to the eight small layers. It follows, therefore, that each horizontal layer of the same thickness, no matter where it lies in the liquid, produces the same pressure, the amount depending upon its thickness and the area of its base. The total pressure of the liquid upon the bottom must depend, therefore, on the area of the base, and its vertical height or thickness—that is, equal to a column of liquid having the same base and the same vertical height. The truth of the theorem so deduced

FIG. 173.



To illustrate the pressure exerted by liquids.

FIG. 174.



Apparatus to demonstrate that the pressure is independent of shape and size of vessel.

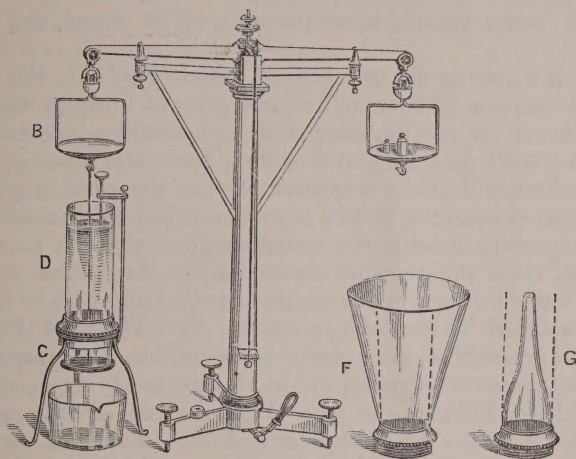
is experimentally verified by the experiment just performed, since the pressure exerted by the columns of liquid in A and B (Fig. 172) are the same, because they have the same base and the same height of liquid above it. That the shape of the vessel has no more influence with regard to the pressure exerted by the water it contains than that exerted by the amount will become, perhaps, more evident if the apparatus (Fig. 174) be filled with water. The level to which the water rises being the same in all the tubes, though of very different shape, proves that the pressure exerted by the water must be the same in all of them. On account, however, of the practical importance of the law of the pressure of liquids, and of the necessity of keeping clear in the mind the distinction between the pressure exerted by the liquid and its weight, let us illustrate the principle involved a little more in detail by means of the apparatus represented in Fig. 175.

This consists of a balance, in one of whose scale pans (A) a known weight is placed, while to the other (B) a wire is attached, terminating in a flat disk (C), which is so exactly applied to the lower opening of the supporting cylinder (D) that it practically constitutes its bottom, being tightly drawn up by the counterpoising weight in A. A known weight being now added to that already in A, and water being gradually poured into the cylinder, by degrees the pressure of the liquid on the disk or bottom increases, and when the pressure so exerted equals the counterpoising weight in A the least excess of water detaches the disk—that is, the bottom of the cylinder falls out, and the water flows out; but, as the pressure is



at once diminished by the outflow, the disk is drawn up again, and adheres closely to the cylinder. The pointer touching the surface of the water marks its level at the moment of equilibrium.

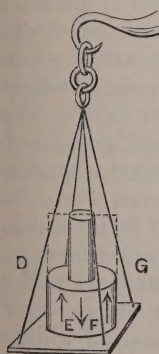
FIG. 175.



Pressure of a liquid on the bottom of the vessel which contains it.

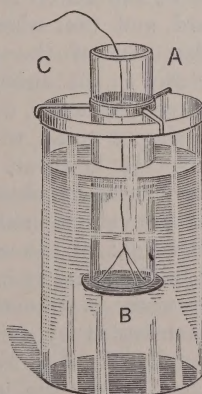
In this experiment it is obvious, as might have been expected, that the pressure exerted by the water upon the bottom is precisely equal to its weight, which was two pounds. Suppose, now, we substitute for the cylinder a conical-shaped vessel (F), with the same sized orifice at the bottom, but with a much wider one at the top, and, therefore, capable of containing more water; nevertheless, if we experiment with the conical

FIG. 176.



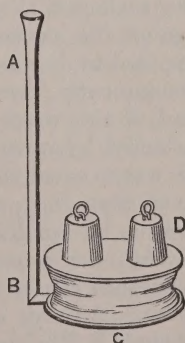
Hydrostatic paradox.

FIG. 177.



To demonstrate the upward pressure exerted by water.

FIG. 178.



Hydrostatic bellows.

vessel as we did before with the cylinder, notwithstanding that the former contains three times as much water as the latter, the pressure exerted by the water upon the bottom, as we see, is the same, being only

two pounds, whereas, the water weighs six pounds. In the experiment with the conical vessel the pressure exerted by the water upon the bottom is, therefore, less than its weight, and the reason is very obvious, since it is only that part of the water within the dotted lines that exerts pressure upon the bottom, the pressure of the remaining extra water, so to speak, being exerted upon the walls of the vessel, and not upon its bottom.

Finally, if we make use of a conical vessel (Fig. 175, G), or of one (Fig. 176) consisting of two cylindrical parts of unequal diameters, of which the lower one has the same sized orifice at the bottom as obtains in the two vessels just used, and holding less water than either of the latter, we shall still find, experimentally, in the same way, that the pressure exerted upon the bottom is undiminished by that circumstance, being two pounds, though the water weighs only one pound. This must be so, since the pressure exerted upon the bottom is due to a column of water having the same vertical height and base as the column of water included between the two dotted lines D and G (Fig. 176)—that is, the pressure of the column of water on the principle of the pressure being exerted equally, and in all directions, is not only exerted upon E F (Fig. 176), or the part of the bottom directly underneath it, but also upon the remaining part of the bottom on both sides of E and F. The total pressure exerted upon the bottom is therefore the same as if there were two extra columns of water (D, G) pressing downward in addition to that upon E F actually present. It will be observed in this experiment that the pressure exerted by the water upon the bottom is therefore greater than its weight. At first sight, this result may appear paradoxical, it being perhaps difficult to comprehend why, if the water in the vessel exerts a pressure upon the bottom, that when the vessel is placed in the scale-pan of the balance that its weight should be only equal to the weight of the water and vessel. The reason, however, becomes at once clear when it is remembered that the pressure of the water is exerted in all directions, upward as well as downward, and that when the vessel is placed in the scale-pan (Fig. 176), that part of the pressure exerted upward against the surface of the vessel in the direction of the arrows, being opposed in direction to the force of gravity, does not appear as weight; consequently, the weight is simply equal to the weight of the vessel and of the water it contains. If, however, this upward pressure be balanced by an equal downward pressure, obtained by an extra quantity of water, equal in amount to the volume included between the dotted lines, then the pressure and weight of the water would be identical—that is, the conditions would be the same as in the first experiment.

That the pressure of the water is transmitted upward as well as downward can be readily demonstrated by the following simple experiment. A large open glass tube (A, Fig. 177), one end of which is ground, is fitted with a thin card (B), to the centre of which is attached a string (C) by which it can be held against the bottom of the tube. The whole is then immersed in a jar of water, and, although the string be allowed to hang over the side of the jar, the card will still adhere to the mouth of the jar, it being kept in this position by the upward pressure of the water.



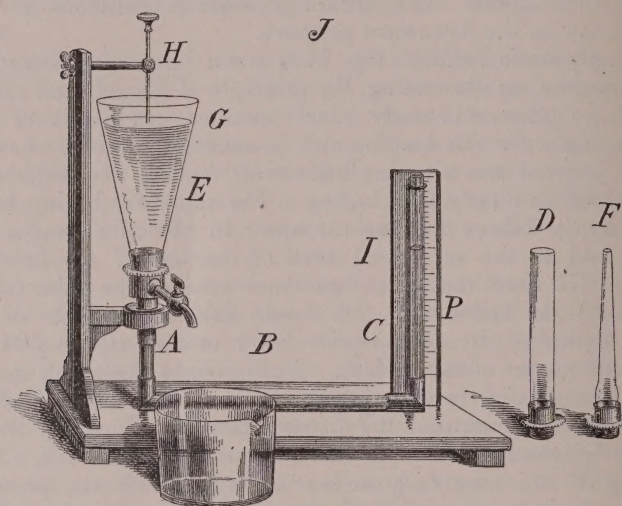
If now water be slowly poured into the tube the disk will still adhere to the latter, not sinking until the height of the water inside the tube is equal to the height outside. Hence, it follows that the upward pressure is equal to a column of water whose area is that of the tube (A), and whose height is the distance from the disk to the outer surface of the liquid. The upward pressure is, therefore, governed by the same law as the downward pressure.

The hydrostatic bellows (Fig. 178) is an interesting instrument in this connection, as illustrating the principle of Pascal, and the manner in which we propose to study blood pressure. It consist of a narrow tube (A) eight feet in length, with a sectional area of one-fourth of an inch, inserted into a square bellows (C) having a superficial area of one hundred and forty-four inches. The apparatus having been filled with water, it follows that, as the water in the tube weighs fourteen ounces, and as the superficial area of the top of the bellows (144 inches) is 576 times that of the sectional area of the tube (one-fourth of an inch), the bellows (D, D) should balance a weight of fourteen ounces multiplied by 576, equals 8064 ounces, equals 504 pounds, which, as a matter of fact, it does. At first sight this result may appear as paradoxical as in the experiment with the cylindrical vessel; it will be observed, however, that the distance through which the 504 pounds upon the bellows are elevated is but the one-sixth of an inch, a fractional part only of the ninety-six inches through which the pressure was exerted. It is only another illustration of what we gained in weight we lost in height, or of a small force acting through a great height being equal to a large force acting through a short one, fourteen ounces falling through ninety-six inches, being equal to 8064 ounces, or 504 pounds, ascending through the one-sixth of an inch. It follows, therefore, that the pressure even of a small quantity of water, if exerted from a sufficient height, will be very great; indeed, Pascal succeeded in bursting a strongly made cask by means of a narrow thread of water forty feet high, and, in this manner, demonstrated his principle of the equality of pressure.

In considering the pressure exerted by two columns of liquid such as obtains in the apparatus (Fig. 172), it will be remembered that only one liquid—water—was used. It is needless to say, however, that if two liquids of different densities, such as water and mercury, were experimented with, the level of the water would stand 13.5 times higher than that of the mercury, the latter being that much heavier, the altitudes of the liquids being inversely as their densities. In other respects, what has been said of the pressure exerted by water will apply equally to mercury or other liquids, and inasmuch as we will make use of a mercurial column as a measure of the pressure exerted by the blood, it will not be superfluous to illustrate first the manner in which we measure by mercury the pressure exerted by any liquid; this we do by means of Haldat's apparatus (Fig. 179). This consists of a tube (A B C) bent at both ends at right angles, one of which is provided with a stopcock (A) on which can be screwed vessels (D, E, F, etc.), of the same height but differing in shape and capacity, D being cylindrical and F conical. The tube A B C is filled with mercury until it reaches the level P. The

vessel *E* is first screwed on, for example, to the end at *A* and water is poured into it until it reaches the level *G*, this level is registered by the movable rod *H*. The pressure of the water in the vessel *E* upon the

FIG. 179.



Haldat's apparatus.

surface of the mercury in the limb *A* will cause the mercury to rise in the tube *G* up to the level *I*, and is there registered by a movable collar. The stopcock *A* is then opened, which allows the water to run out of the vessel *E*, which is then removed and is replaced by the vessels *D* and *F*; these, in turn, are filled with water up to the level *G*, when it will be observed that the mercury which had in the meantime, in each case, fallen to its original level in limb *A*, rises again to the level *I* the same as before, thus proving that the pressure exerted by the water upon the mercury is, as we have already seen, independent of the quantity of the water and of the shape of the vessel, but is equal to the weight of a column of water whose base is the surface of the mercury *M* beneath the stopcock in limb *A*, and whose altitude is the height (*A G*) of the level of the water above the surface of the mercury; that is, the pressure of the water (*P*) equals altitude (*A G*) multiplied by area (*M*). The height of the water being the same in *D F* and *E*, and the surface of the mercury (*M*) representing the area in each case, the product of *A G*  $\times$  *M* must give the pressure exerted by the water in all three vessels, which we have just seen is the case, the column of mercury being the same in both experiments.

The column of mercury is then the measure of the pressure exerted by the water in *D*, *F*, or *G* sustaining it. It is obvious that we must double *P I* as the mercury is proportionally depressed in the other limit of the tube. It is by means of the hydrostatic principles that we have illustrated somewhat in detail that Stephen Hales, in the early



part of the last century, first determined the cardiac blood pressure in a living animal with anything like accuracy, and estimated what it would probably be in man. It is true that before the time of Hales the subject of blood pressure had been studied by physiologists and physicists, among others, notably by Borelli.<sup>1</sup> As this distinguished mathematician's calculation was based, however, upon purely theoretical data, and as his estimate of the force of the heart being equal to 180,000 pounds was such a gross exaggeration of the truth, it appears strange now that any importance should ever have been attached to it. Indeed, any reference to Borelli's views as regards blood pressure has at the present day only an historical interest. Hales's method was, however, logical in principle, and, indeed, with certain modifications in the construction of the apparatus, is the one made use of at the present day. Hales's method<sup>2</sup> of experimenting was as follows: A living animal, a horse, for example, having been firmly secured, a large artery, like the femoral or carotid, was exposed, and, after having been ligated, was opened. A brass tube was then inserted into the vessel, to which was adapted a glass tube ten feet long. The connection between the brass and the glass tube was made by a brass pipe, and in some cases by a portion of the trachea of a goose, the latter being used on account of its pliancy so that no disarrangement would ensue through the struggles of the animal. The tube having been inserted into the femoral artery, for example, the blood was observed to rise in the glass eight feet three inches above the level of the left ventricle of the heart. In the case of the carotid artery the blood rose even higher, attaining a height of nine feet six inches, or 144 inches. In order to estimate the pressure or force sustaining such a column of blood, just as in the case of the experiment with the water and the mercury, or with the bellows, the altitude 144 cubic inches must be multiplied by the internal surface of the left ventricle of the horse's heart, or the area. Hales determined the area of the left ventricle of the horse's heart by injecting it with hot wax, then the wax, when cold, was removed and small pieces of paper properly cut were placed upon it until the wax was perfectly covered; the small pieces of paper were then removed to a sheet of paper which was ruled off into squares, and in this way it was estimated that the inner surface of the ventricle, or the area needed for the calculation, was equal to 26 inches, deducting <sup>1 inch</sup> ~~1 inch~~ for the orifice of the aorta. The pressure or the force of the liquid, in this case the blood in the carotid artery, being independent of the quantity and the shape of the vessel containing it, but equal to the altitude of the column of the blood multiplied by the area or its base, the product of 144 inches by 26—that is, 2964 inches of blood will be the pressure or force which the ventricle sustains at the moment of its systole. Now, as a cubic inch of blood weighs 267.7 grains, the pressure of the blood amounts to  $267.7 \times 2964$ , or 7,933,628 grains, which is a little over 113 pounds, there being 7000 grains to the pound. On the supposition that the blood would rise  $7\frac{1}{2}$  feet high in a tube

<sup>1</sup> De Motu Animalium, Pars Secunda, p. 104, Prop. lxxiii. Lugd. Bat., 1685.

<sup>2</sup> Statistical Essays, vol. ii. pp. 1, 2, 14, 15, 19, 20, 21, 39, 40. London, 1740.

inserted into the carotid artery of a man, and that the internal area of the left human ventricle is equal to 15 square inches, Hales estimated by the method just mentioned, that the pressure on the left ventricle at the moment of contraction would amount to 55 pounds (25 kilo.). This estimate is too low, both in the case of man and the horse, as shown by the later investigations of Poisseuille, Volkmann, etc., to be described presently, that the blood would probably rise in a tube placed in a carotid artery of a man, as in that of the horse, to the height of 9 feet, there being but little difference probably in this respect as regards these mammals. Indeed, Volkmann<sup>1</sup> has shown that even in the chicken the blood rises as high in some instances as in the dog and the horse. The area of the left ventricle also, as determined by Collin,<sup>2</sup> is greater than that given by Hales. Further, Haughton,<sup>3</sup> by a different method from that of Hales, calculated that the cardiac blood pressure in man ought to be about the same as that observed in the horse, his method being based upon a knowledge of the distance to which a divided artery will spurt, which in the case of man was learned by Haughton through a surgical operation, the force with which the heart contracts to produce such an effect being deduced from this data.

Modern investigation, as we shall see, has shown that the blood pressure is influenced by conditions unknown to Hales, nevertheless his original experiment is to this day the most striking way of demonstrating it, and his application of hydrostatical principles in measuring it is the method since so successfully made use of by Poisseuille, Volkmann, Ludwig, and others.

It is not so much, however, the pressure that the heart sustains which the physiologist wishes to determine as the actual force with which the heart drives the blood into the aorta at each ventricular systole. The difference between the action of the heart and that of the hydrostatic apparatus we have shown, in which the large glass tube and bellows represent the aorta and heart, is that the heart, like any other muscle, exerts itself according to the resistance to be overcome. Thus, if we raise a pound with our hand, the muscles of the extremity make a greater effort than when we raise a feather, so according to the resistance, for example, offered by the capillaries to the efflux of the blood into them from the arteries, will the heart contract more forcibly, and the blood-pressure will rise. It is evident, then, that the possible force of the heart and the actual force usually exerted may differ very much in amount. Before demonstrating this experimentally let us explain the hæmadynamometer, the apparatus by means of which blood pressure is usually studied at the present day, and then compare the arterial with the cardiac pressure. The hæmadynamometer, so called from the Greek words hæma, blood, dynamis, force, and metron, measure, is essentially a mercurial manometer adapted to measure the blood pressure, hence the name given to the instrument by Poisseuille,<sup>4</sup> who first, in 1828, made use of it for this purpose. The apparatus that we shall use (Fig. 180) is the same as Poisseuille's, with some modifications.

<sup>1</sup> Die Hæmodynamik, S. 177.

<sup>2</sup> Animal Mechanics, p. 40. London, 1873.

<sup>3</sup> Journal de physiologie de Magendie, tome viii. p. 272, 1828.

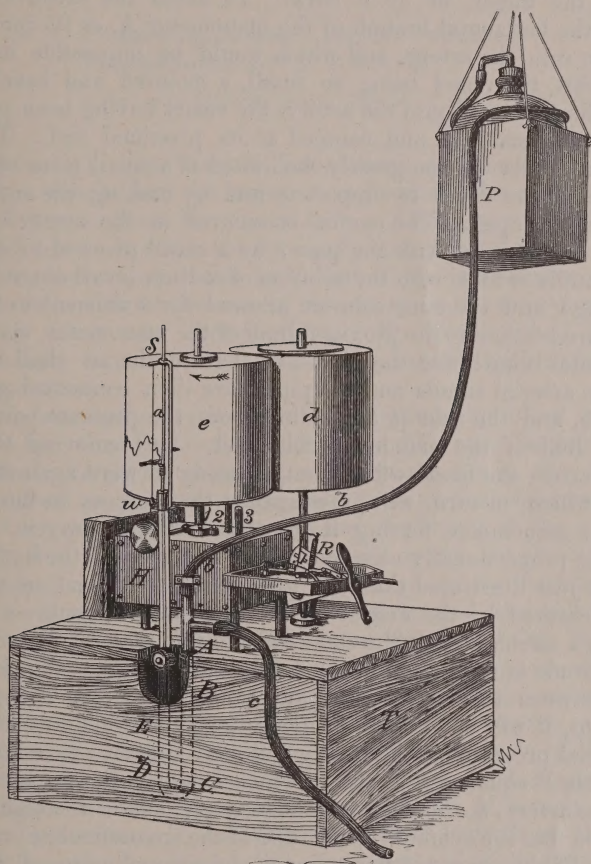
<sup>4</sup> Comptes Rendus, xlvii. tome 155.

hæma  
dynamometer



It consists of a U-shaped glass tube (B C D E), of which the distal or ascending limb (D E) is longer—32 cm. (12½ inches)—than the proximal or descending one (B C)—20 cm. (8 inches). The tube has a diameter

FIG. 180.



The mercurial kymograph. *a*. Vulcanite rod of floating piston. *b*. Tube which communicates with the pressure bottle. *c*. Tube which communicates with the artery. *d*. Feeding cylinder. 1. First axis, which revolves once in a minute. 2. Second axis, which revolves once in ten seconds. 3. Third axis, in a second and a half. The instrument is furnished with other cylinders suitable for the reception of single bands of glazed paper, the surface of which can be blackened after they are fixed on to the cylinders, by causing the latter to revolve over the flame of a petroleum lamp. These cylinders can be fitted on to either of the axes 1, 2, or 3, and are always used when it is necessary to employ a rapidly moving surface, as—*e. g.*, for tracing the curves of muscular contraction. (SANDERSON.)

of 1.25 cm. ( $\frac{1}{2}$  inch.). From the distal branch B is given off a short horizontal one A, 2.5 cm. (1 inch), by means of which the manometer is put in communication with the artery whose blood pressure we wish to determine, and which, in this case, will be the carotid artery of the rabbit. The U-shaped tube being clamped in a vertical position, perfectly clean and dry mercury is poured into it until the mercury reaches a given level in the two limbs. To prevent the blood coagulating

that which will come from the artery a saturated solution of sodium carbonate or subcarbonate is allowed to flow from the pressure-bottle P through the tube *b b* into the proximal end B of the manometer, and through its horizontal branch (A), to which is connected by a short piece of tubing a glass tube, or leaden pipe (*c*), the latter being stopped temporarily by the finger, or by a cork. To avoid the inconvenience of inserting the horizontal branch of the manometer A, or its continuation the pipe *c*, into the artery, and which would be impossible in the case of the rabbit, the vessel being so small, a pointed and bevelled glass canula is first inserted into the artery, the vessel having been previously ligated at its distal end, and clamped at its proximal end. The insertion of the canula will be greatly facilitated if a small piece of card be placed under the vessel to support it, and by making the opening for the canula V-shaped. The canula is secured in the artery by a ligature, and is connected with the pipe *c* by a small piece of tubing. The arterial canula is filled with the solution of sodium bicarbonate by means of a syringe, and the same solution allowed for a moment to flow from the pressure-bottle into the proximal limb of the manometer, and through its horizontal branch and the pipe *c*, so that all the air shall be driven out. The arterial canula and the pipe *c* are then connected as quickly as possible, and the tube (*b b*) leading from the pressure-bottle to the proximal limb of the manometer clamped. On removing the clamp from the artery the blood will jet out, pressing forward against the soda solution, which, in turn, will press against the mercury in the proximal end of the manometer, forcing it downward, the mercury in the distal limb being proportionally elevated. It is evident from the hydrostatical principles just illustrated that the pressure of the blood in the artery will be measured by the weight of the column of mercury, whose base or area is a circle, having the same diameter as that of the artery, and whose altitude is the height of the column of mercury—that is, the difference between the two levels F and G, and which, in this particular experiment, it will be observed, amounts to 90 millimeters (3.6 inches). The arterial pressure can be briefly and conveniently expressed then by the formula  $P \text{ equals } \pi R^2 h W$ , in which  $P$  equals the pressure,  $R^2$  the area of the artery,  $h$ , the height of the mercury, and  $w$  its weight, it being understood that the symbol  $\pi$  is the ratio of the circumference to the diameter, and  $R^2$  the square of the radius of the circumference of the artery, and that the product of  $\pi$  by  $R^2$  gives the area. Thus, the diameter of the aorta at the level of the semilunar valves, in a man aged twenty-nine years, being 34 millimetres (1.3 inches), as was found to be the case by Poyseuille,<sup>1</sup> the radius  $R$  would be 17 millimetres, and the square of  $R^2$  289, the latter multiplied by  $\pi$ , or 3.1416, will give about 907 millimetres (1.4 inches) as the area of the aorta at the level of the semilunar valves. The area, or 907 millimetres, multiplied by 160, or the probable height to which the mercury would be elevated could the manometric tube be inserted into the human aorta, gives 145120 millimetres as the volume of mercury sustained by aortic pressure. On the suppo-

<sup>1</sup> Op. cit., p. 304.



sition that 1 millimetre of mercury weighs about  $\frac{1}{73}$  of a gramme (0.21 grain), 145120 millimetres will weigh  $\frac{145120}{73} = 1988$ , or nearly 2000 grammes, or nearly 2 kilogrammes—that is, about 4.4 pounds. Substituting the value in the formula given for the pressure, we have

Pressure equals area  $\times$  height  $\times$  weight.

Pressure equals  $\pi \times R^2 \times h \times W$ .

$$4 \text{ lbs.} = 3.1416 \times 289 \times 160 \times \frac{1}{73}.$$

It may be said, then, that the actual force or pressure under which the blood is driven into the aorta at each ventricular systole amounts to about 4.4 pounds on the square inch. As a general rule, however, the blood pressure is estimated by simply measuring the height to which the mercury is elevated in the distal limb of the manometer, and doubling the result, without the area of the artery or the weight of the mercury being taken into consideration. By that method the aortic pressure would be estimated as amounting to 160 millimetres, or only about 2 grammes.

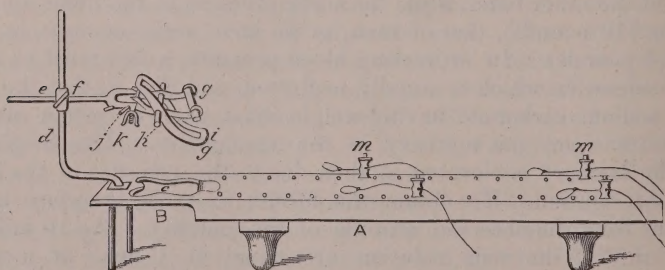
The disadvantage of such a manner of estimating blood pressure is due to the fact already mentioned that the difference between animals as regards the height to which the mercury will rise in the manometer is not as great as perhaps might have been at first imagined. Since the blood pressure depends not only on the height of the mercury in the manometer, but also on the area of the artery, we should expect to find, as indeed is the case, that while the height of the mercury is about the same in three different species of animals, that the blood pressure may be very different. Thus in the horse, sheep, and dog, the mercury will rise in the manometer to about the same level, on an average 150 millimetres (6 inches). As the aortic force or blood pressure, however is equal to this height multiplied by the area of the aortic orifice, it is evident that the pressure will be proportional to the size of this orifice, and will therefore be greatest, other things equal, in that animal which has the largest aorta. Thus the blood pressure of man as estimated simply in millimetres of mercury differs but little from that of the horse; on the other hand, while the aortic pressure in the horse amounts to 5 kilo. (10 pounds), that of man, as we have seen, amounts to only 2 kilo. (4 pounds). In estimating blood pressure, a fact must be taken into consideration which is usually neglected, and that is, that the solution of sodium carbonate having weight must exert a certain amount of pressure upon the mercury in the manometer. The height to which the mercury is elevated is then due to the pressure of the blood and of the solution. To obtain the former we must therefore deduct the latter from the observed altitude of the mercury. As 10 millimetres ( $\frac{2}{5}$  in.) of the soda solution are equal to 1 mm. of mercury for every 10 mm. of the soda solution in the proximal limb of the manometer we must deduct then 1 mm. of mercury from the altitude of the mercury in the distal limb of the manometer. As a general rule, the amount of the soda solution in the proximal limb of

the manometer is so small that the effect of its weight upon the mercury need not be considered. Thus, in determining the blood pressure in the carotid artery of the rabbit it will be noticed that the solution of soda amounts to only 5 mm. ( $\frac{1}{5}$  in.), and therefore only  $\frac{1}{2}$  mm. must be subtracted from the 90 mm., or the observed altitude of the column of mercury, to obtain the arterial pressure. In using certain kinds of manometer, however, as we shall see, the amount of the soda solution being greater the influence of its pressure becomes more appreciable. It will be observed, also, that the pressure bottle containing the solution of sodium carbonate is suspended at a height of about 2 metres (6.5 feet) above the manometer, and that it can be elevated or depressed as desirable. The object of this is that having learned by experience to about what height the mercury will be elevated by the arterial pressure, we make use of the soda solution not only to prevent the coagulation of the blood, but also to exert pressure upon the mercury to the same extent as the arterial blood will do. As soon as the clamp is removed from the carotid artery the blood at once then exerts its pressure upon the soda solution, but advances only a little way in the tube *c*, loss of blood as well as coagulation being thereby prevented. The pressure of the blood is then transmitted to the soda and thence to the mercury; if the pressure bottle has not been sufficiently elevated, then the level of the mercury will rise in the distal limb of the manometer, and if too much elevated the reverse will be the case. The effect of the arterial pressure will therefore be the same as if exerted directly upon the mercury.

In speaking of the connecting tube *c*, it was mentioned that it should be of glass and preferably of lead. The reason of this is now very evident. Did the tube consist of an extensible material the pressure of the blood would be exerted to a great extent upon the walls of the tube rather than upon the soda solution, and indirectly therefore not upon the mercury.

Various methods are made use of by physiologists to secure firmly the animals to be experimented upon. In this instance we make use of

FIG. 181.



Czermak's rabbit support. (SANDERSON.)

Czermak's rabbit support, and as the apparatus when sufficiently large, is equally convenient for other animals, and as we shall frequently



have occasion to use it, a short description seems advisable. It consists (Fig. 181) of a firm wooden stand A, 1 metre (3.2 feet) long and 22 cm. (9 in.) wide. The end B with the large opening *c* is made stronger than the rest of the stand by an iron plate into which an iron rod (*d*) bent twice nearly at right angles is screwed. This rod carries a movable brass ring through which passes horizontally an iron rod *f* movable in all directions, and which bifurcates at the end, the two ends of the horizontal rod being adjustable to the frame-like clamp through which passes the rod *h* in a direction at right angles to that of the horizontal rod *f*, the rod supporting a second clamp of the same general form as the first one, and which by means of the screw *k* can be brought near to the latter. The animal being placed upon its back, and resting upon a mattress, the neck supported by a cylindrical cushion and the extremities fastened by strings to the pegs *m m*, the rod *h* is placed between the teeth and the screw *k* so adjusted that while the clamp *g* presses upon the lower jaw the clamp *g* will press upon the head. In this way the animal is firmly held, and yet does not receive the slightest injury.

We have just seen that the aortic pressure in man amounts to nearly 2 kilo. (4.4 pounds) to the square inch. Now since the pressure exerted upon the mass of a liquid is transmitted undiminished equally in all directions, and acts with the same force on all equal surfaces according to the principle of Pascal, to obtain the cardiac pressure we have only to multiply the 2 kilo. or the aortic pressure by the internal area of the left ventricle, or 38.1 centimetres (15 in.), which gives 30 kilo. (66 pounds). This result, it will be observed, agrees very closely with that of Hales. This should be so, since the hydrostatic principle made use of by both Hales and Poisseuille in determining the cardiac and aortic pressure was the same. It was for this reason on account of the application of hydrostatic principles in the study of blood pressure that we illustrated these principles so much in detail.

If now the hydrostatic bellows be compared to the heart and the aorta, it is obvious that the aortic pressure corresponds in the bellows to the small force acting through a great height in the narrow tube, while the cardiac force is the great force acting through the small height corresponding to the force in the bellows. It must not be forgotten, however, that the pressure in the heart may vary according to circumstances due to its inherent contractility whereas the pressure in the bellows is constant for the same quantity of water otherwise the principles involved are the same.

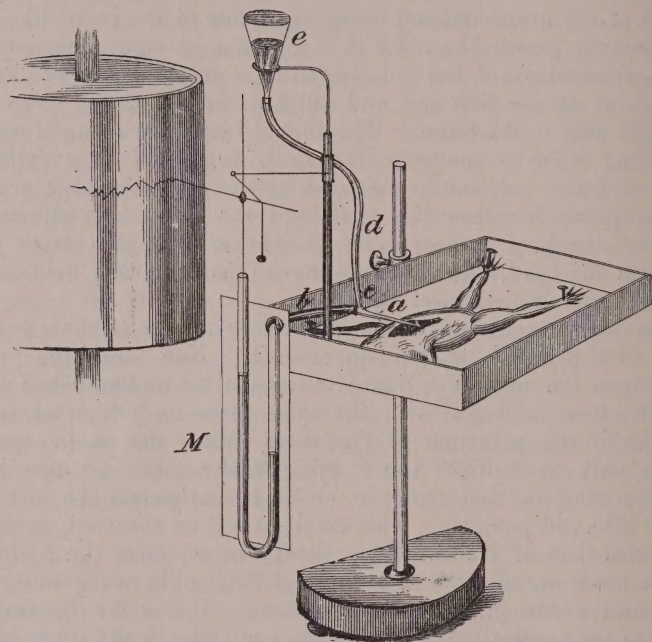
That the cardiac pressure is greater than the aortic is shown by the fact that with each ventricular systole the mercury rises in the manometer, falling again with the diastole, the mean arterial pressure being, as we shall see, the level between these extremes. Further, as we have just mentioned, and which we will now demonstrate, the cardiac pressure will be greatly increased beyond that which we may consider as normal, according to the resistance to be overcome. This is usually shown by means of Coats's apparatus,<sup>1</sup> or by that described by Marey,<sup>2</sup>

<sup>1</sup> Described in Handbook Phys. Lab., p. 263, plate xci.

<sup>2</sup> Circulation du Sang, 1881, p. 70, fig. 28.

but, as both these methods involve taking the heart out of the animal, and as we wish to show the phenomena, the heart being in situ, we will make use of the convenient little apparatus (Fig. 182) as arranged by Dr. A. P. Brubaker, for studying blood pressure in the frog. This

FIG. 182.



Brubaker's frog manometer.

consists of a mercurial manometer *M* like that we have used in determining the blood pressure in the rabbit, only that it is smaller. The arterial canula differs, however, from the one used in that experiment. In this instance the end *a* of a J-shaped glass tube is inserted into the bulbus arteriosus of the frog, the end *b* being adjusted to the proximal end of the manometer, while the stem *c* is connected by the tube *d* with a funnel *e* containing a solution of sodium carbonate. The funnel corresponds to the pressure bottle in the experiment with the rabbit. The frog is secured to a piece of cork, which rests within the stand supporting the manometer; the stand can be raised or lowered upon the vertical rod; the latter also supports, by the horizontal rod, the funnel. Having first determined the normal blood pressure, it will then be observed that as the tube *d* is compressed, an obstacle being thereby interposed to the flow of blood from the aorta, the pressure will be increased, the mercury rising in the distal limb of the manometer, thus showing that the force which the heart exerts is proportional to the resistance to be overcome.



While the flow of the blood through the arterial system generally is influenced by the length of the vessel, friction, etc., the capillary system, as we shall see, is a constant source of resistance. In proportion to the fulness of the capillaries a greater or less obstacle is offered to the flow of the arterial blood. The force that the heart exerts must then vary according to the resistance to be overcome. It is hardly necessary to state that the constriction of the tube in the last experiment would represent a capillary obstruction in the living animal. Theory and experiment, therefore, agree in showing that the amount of force which the heart usually exerts is far less than the possible force that can be put forth if occasion demands it. Very great differences are found, also, among animals, as regards the proportion of the cardiac to the arterial pressures. In the rabbit, for example, the force of the left ventricle exceeds but little that of the aorta, whereas, in the horse, the excess of the cardiac pressure as compared with the arterial is very marked. Thus, by means of his cardiometer, Bernard<sup>1</sup> has shown that the arterial pressure in the rabbit being 91 mm. (3.8 inches), with each ventricular systole the mercury rose to 100 mm. (4 inches), the cardiac pressure being only 5 mm. greater than the arterial. On the other hand, in the horse, the arterial pressure being 100 mm. (4 inches), the cardiac pressure was 65 mm. greater, the mercury rising to 175 mm. (7 inches) with the systole.

Just as we have seen the pulse gradually disappearing as we recede from the heart, so, for the same reason, we should expect to find this excess of cardiac over arterial pressure becoming less and less as we pass toward the periphery. Experiment confirms in this respect what theory would lead us to expect. Thus, Volkmann<sup>2</sup> has shown that, while in the carotid artery of the dog the excess of the cardiac pressure, as compared with the arterial, amounts to 37 mm. (1.4 inches); in the metatarsal artery the excess amounts to only 1 mm. ( $\frac{1}{25}$ th of an inch).

In making the distinction between cardiac and arterial pressures, it must not be forgotten, however, that the latter is only the delayed effect of the former, since the cardiac pressure exerted during the previous systole in distending the arterial wall is restored during the diastole to the circulation through the elasticity of the artery as arterial pressure.

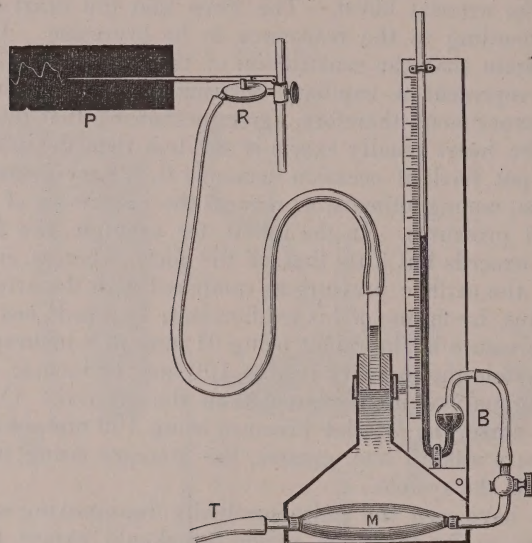
The cardiometer we make use of in demonstrating the difference between cardiac and arterial pressure is that shown in Fig. 183, as made by Verdin, of Paris. It is but a slightly modified form of the cardiometer used by Magendie and Bernard, and consists of a metallic vessel containing water, within which is suspended an elastic capsule, (M), communicating at one end (T) with the artery whose pressure is to be determined, and at the other end with a delicate mercurial manometer (B) for registering the pressure. The upper part of the vessel is closed with a cork, through which passes a glass tube, into which the water rises, and which transmits to the registering tambour R the distention of the capsule M due to the varying cardiac pressure. The arterial pressure, however, when once attained, remains constant, the constriction at the

<sup>1</sup> *Système Nerveux*, tome i. pp. 283, 286.

<sup>2</sup> *Die Hæmodynamik*, S. 167.

bottom of the mercurial manometer B offering such a resistance to the rise of the mercury that the intermittent action of the heart is not felt.

FIG. 183.



Cardiometer. (MAREY.)

Having described the manner in which the mercurial manometer is used in determining the force of the left ventricle, a few words will suffice as to the force exerted by the right ventricle. According to Marey<sup>1</sup> and Chauveau, on the average the force of the right ventricle is about one-third of that of the left; the force of the right auricle being about one-tenth that of the right ventricle, it is about 1.30 to 1.7 of the left ventricle. Inasmuch as the left auricle is inaccessible in a living animal to experimental investigation, nothing positively is known as to the pressure exerted by it. It is reasonable to suppose that it is equal to that of the right auricle.

A great advance was made by Ludwig,<sup>2</sup> in 1848, in the manner of investigating blood pressure, by his invention of the kymograph (Fig. 180). This consists of a mercurial manometer like that of Poisseuille, in the distal limb of which is placed a vertical rod (*a*) the lever-end of which terminates in a concave cup-shaped float, and rests upon the convex surface of the mercury, while the upper end of the vertical rod projects out of the upper open end of the distal limb of the manometer, and carries a delicate sable brush, wetted with ink, or a pen of glass, the point of which rests against the cylinder *e*. The vertical rod is kept in the perpendicular by the support *s*, through which it passes, and the brush or pen in contact with the cylinder by the weighted string *o*. The cylinder *e*, 16 cm. (6.5 inches) high, and 50 cm. (20

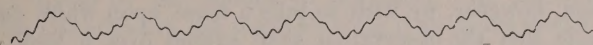
<sup>1</sup> Op. cit., p. 115.

<sup>2</sup> Muller's Archiv.



inches) in circumference, is covered with either white or smoked paper. With every oscillation of the mercury in the distal limb of the manometer, the rod *a* is elevated or depressed, and a vertical line is made upon the cylinder by the brush or pen. If now the cylinder is made to revolve at a uniform rate, the vertical mark will become a curve, like that represented in Fig. 184, and we obtain a graphic representation of the blood pressure in this of the rabbit, hence the name

FIG. 184.



Trace of blood-pressure in rabbit.

kymograph—from kumos, a wave, and grapho, to write—the name given to the instrument by Volkmann,<sup>1</sup> who was among the first to use it successfully. Ludwig<sup>2</sup> tells us that the idea of the recording pen, etc., was suggested to him by a similar contrivance made use of by Watt for registering pressure in the steam engine. The immense importance of Ludwig's invention cannot be exaggerated, for, by means of the kymograph, the study of blood pressure became far more exact than had been possible previously.

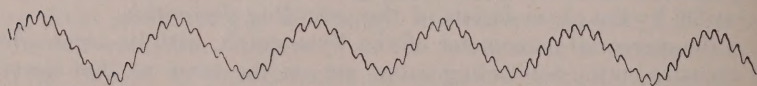
Slight variations in the oscillation of the mercury, for example, which were entirely inappreciable in the hæmadynamometer, became perfectly apparent when graphically recorded upon the revolving cylinder. The great merit of Ludwig's invention did not consist simply in the application of the kymograph to the study of the blood pressure, but the application of the graphic method in the investigation of the circulation of the blood generally, and, indeed, of all physiological phenomena. In truth, it is not saying too much that the study of physiology experimentally has been revolutionized by it, results having been obtained by the graphic method, as we have already seen, which had been considered impossible by the physiologists of the preceding generation.

As the mercurial manometer of the kymograph, with its accessories, the pressure bottle, connecting tubes, etc., is the same as that already described, it is only necessary to say that the mercurial manometer, when used as part of the kymograph, is firmly clamped to the table (*T*) supporting the cylinders, and that the vertical rod in its distal limb is so adjusted that the brush or pen which it carries remains in contact with the cylinder. The latter in the instrument we use, made by Hawksley, of London, is moved by clock-work contained in the box *H*, and its motion made uniform by the Foucault regulator (*R*). This consists of two fans, which, when the velocity is increased through the friction engendered, expand and so retard the motion, and when the velocity diminishes contract again, and so offering less resistance it increases again, the fans being approximated and separated by an elastic spring. There are three axes (1, 2, 3) connected with the clock-work, and according to the one on which the cylinder is placed the rate of its revolution can be varied. Thus, when the cylinder is placed upon the first axis it makes

<sup>1</sup> Die Hæmodynamik.<sup>2</sup> Physiologie, 1861, S. 163, Band. i.

one revolution in one minute fifty-two seconds, or seventy-five seconds upon the second axis, one revolution in twelve seconds; upon the third axis one revolution in two seconds. It will be observed, therefore, that when the cylinder is on the third axis it revolves nearly forty times as rapidly as upon the first. When the cylinder used is that covered with smoked paper, it is held on the axis connected with the clock-work by a vertical rod passing from its centre upward into the frame, and which is screwed on to the box. By means of this vertical rod the cylinder can also be elevated or depressed through a height of several centimetres. When, however, we wish to take a trace upon white paper, and it is desirable that the observation shall extend over a long period of time as possible, then a somewhat different arrangement is made from that just described. We then use two cylinders (Fig. 180, *e*, *d*), one of which (*e*) is to record the trace, and which, resting upon the axis connected with the clock-work, is supported from above by a frame, not represented in the figure, which, like the other frame, can also be screwed on to the box. The other cylinder (*d*) is covered with white paper rolled around it by machinery, and in quantity sufficient to last for several hundred observations. This cylinder acts as a feeder to the recording one, for, as the latter revolves, it unwinds the white paper around the former, the paper being kept smooth by two little ivory wheels on the frame (not represented in Fig. 180). Having explained the construction of the kymograph, let us consider now the traces of blood pressure of the cat, turtle, frog, for example, as recorded by it, and point out some of the results obtained by their study, and which would have been impossible had we limited our study of blood pressure to the use of the mercurial manometer only. By an examination of Fig. 185, illustrating the kymographic trace of the blood pressure in the cat, recorded upon the smoked paper, it will be observed that the

FIG. 185.



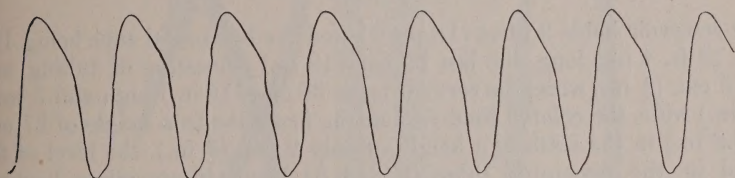
Trace of blood pressure in cat.

trace consists of a number of large curves, each of which is made up of smaller ones. The large curves extending from crest to crest of the wave, being to a certain extent respiratory in origin, their relations to inspiration and expiration will be considered hereafter. For the present, however, it may be said, by the graphic method it can be shown that, during a part of the period of inspiration, the blood pressure is increased and during a part diminished, and that in the same way the blood pressure is both diminished and increased during expiration. The small curves are cardiac in origin, each small curve corresponding to a heart beat, the elevation being caused by the systole, the depression by the diastole. If the pen be watched during these oscillations, it will be noticed that there is an average height above and below which the pen is elevated and depressed with each cardiac beat. This average height represents the mean arterial pressure. To express this in millimetres of mercury we



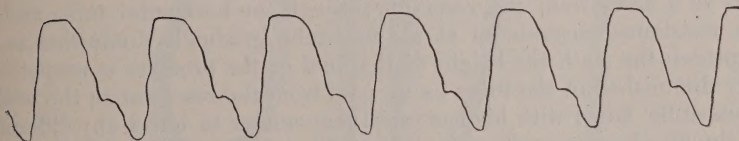
must measure the distance or ordinate between the line representing the average height and the straight line, or abscissa, representing the height at which the pen was elevated by the mercury under the influence of the atmospheric pressure only, before the blood pressure had exerted any force and then double this distance; while to estimate the cardiac pressure in millimetres of mercury we must add to the mean arterial pressure twice the distance of the excursion of the pen during the small oscillation. If we wish to get the mean of either the cardiac or the arterial pressure of a number of pulsations, we must add up the ordinates and divide by the number of ordinates. As pulmonary respiration is far less active in the turtle and frog than in the rabbit naturally, we should not expect to find respiration influencing the form of the curve of blood-pressure in these animals to the same extent as in the mammal. The large curves are then absent in the traces represented in Figs. 186 and 187;<sup>1</sup> the small curves are, however, quite as distinct and

FIG. 186.



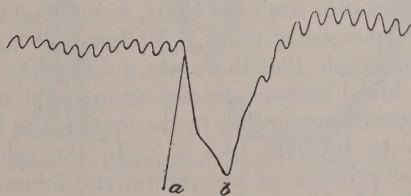
Trace of blood pressure in turtle.

FIG. 187.



Trace of blood pressure in frog.

FIG. 188.



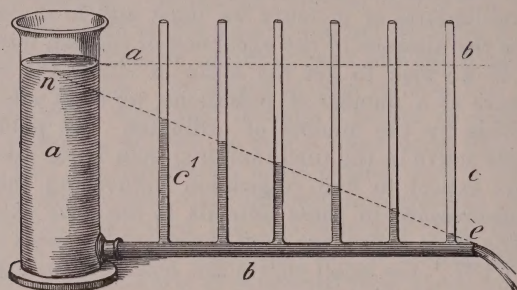
Influence of cardiac inhibition on blood pressure. Current sent into pneumogastric nerve at *a*, shut off at *b*. First, there is a rapid fall, and when the heart beats return, the mercury rises by successive leaps to the normal.

have the same significance as those in Fig. 185. Assuming that the blood flows through the arteries according to hydraulic laws we should expect to find the pressure diminishing as we recede from the heart to the periphery. Thus, if we watch the colored fluid as it flows from the reservoir (*a*, Fig. 189) through the horizontal tube *b*, it will be observed

<sup>1</sup> In the case of the frog the manometer used was smaller than in the case of the rabbit.

that the height to which the fluid rises in the vertical tubes  $c^1$  and  $c$ , inserted into the horizontal one gradually diminishes as we recede from the first ( $c^1$ ) to the sixth tube ( $c$ ). In the present experiment, where

FIG. 189.



Decrease of pressure in tubes of equal calibre.

the reservoir holds 9 litres (18 pints), and the horizontal tube being 120 cm. (3 ft. 4 in.) long, the last 25 cm. (10 in.) consisting of tubing, and 01.5 cm. ( $\frac{1}{2}$  in.) wide, the vertical tubes 38 cm. (15 in.) high and 5 mm. ( $\frac{1}{5}$  in.) wide, the colored fluid rose in the first tube to a height of 27 cm. (10.8 in.) in the sixth to a height of only 9 cm. ( $\frac{3}{4}$  in.), the level of the fluid in the remaining tubes (2, 3, 4, 5) being intermediate between these extremes. This difference in the level of the fluid in the vertical tubes is caused by the resistance due to friction which the fluid encounters as it flows from the reservoir through the horizontal tube, and as the resistance encountered at the first tube gradually diminishes as we approach the sixth the height of the fluid or the pressure is proportionally diminished in the tubes as we pass from the reservoir to the outlet. Poisseuille<sup>1</sup> failed with his mercurial manometer to detect any difference in the blood pressure of arteries situated at different distances from the heart, such as theory indicated should have been found. Indeed, the difference in the blood pressure of two arteries, seen even when one is situated at a considerable distance from the heart, is too slight to be appreciable by the mercurial manometer alone. Volkmann,<sup>2</sup> however, showed by means of the kymograph, that there was a difference of 7 mm. of mercury between the blood pressure in the carotid and metatarsal arteries of the dog, the pressure amounting in the first case to 172 mm. (6.8 in.), and in the latter to 165 mm. (6.6 in.) In the rabbit the difference between the blood pressure in the carotid and femoral arteries is only about 5 mm. ( $\frac{1}{5}$  of an inch); in the calf, however, the difference amounts to 26 mm. (1.04 in.).

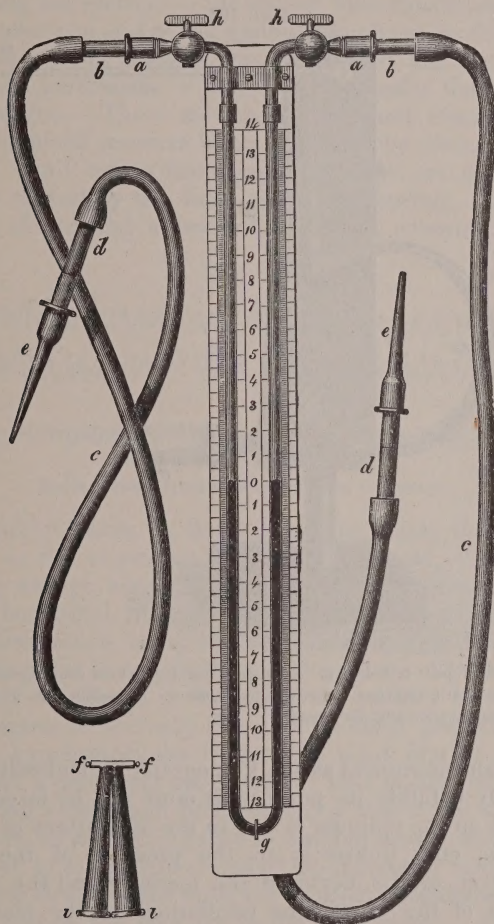
It is not only desirable that we should know whether there exists any difference in the blood pressure of two arteries like the carotid and metatarsal, but also if the pressure in two arteries like the two carotids or the two crurals is equal or different. To investigate this, or if we want to determine the difference between the pressure in an artery and a vein, the carotid and the jugular vein, for example, we make use of the differential manometer of Bernard<sup>3</sup> (Fig. 190). This consists of a U-shaped glass

<sup>1</sup> Op. cit., p. 37.<sup>2</sup> Op. cit., S. 167.<sup>3</sup> Systeme Nerveux, tome i p. 281.



tube firmly supported upon a stand which carries a graduated scale, and by means of which the tube is filled with mercury to a certain level. The two ends of the U-tube are adapted to lead pipes which are connected with the pressure bottle containing the solution of

FIG. 190.

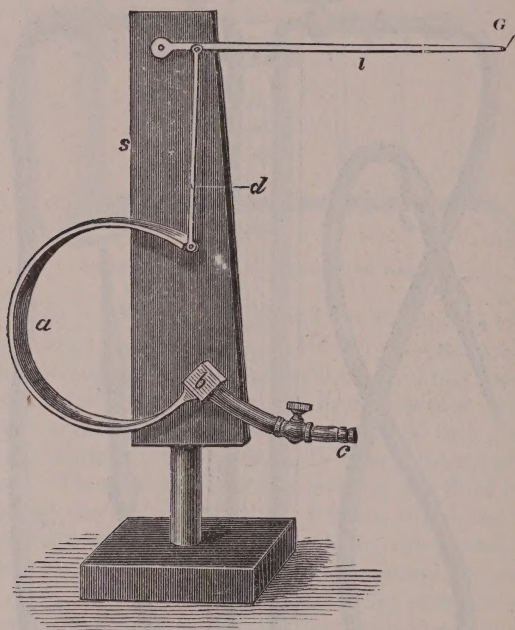


Differential manometer of Bernard. (CARPENTER.)

soda, and at *e e* with arterial canulæ to be inserted into the vessels to be examined. By means of the stopcocks either one or both the vessels can be placed in communication with the manometer. Suppose, for example, we have inserted by means of the arterial canula the two ends of the manometer into the carotids of a rabbit. Having opened both stopcocks and removed the clamps from the arteries and allowed the blood to press against the solution of soda, it will be observed that the level of the mercury remains unchanged, showing, therefore, that the blood pressure in the two arteries is the same. If now one of the stop-

cocks be closed, at once the mercury will rise in the limb of the tube of the corresponding side, and by doubling the height to which the mercury is elevated, and deducting 1 mm. for every 10 mm. of solution of sodium carbonate used, we obtain the blood pressure of the artery on the side where the stopcock remained opened.

FIG. 191.



Fick's spring kymograph. *a*. C-spring. *s*. Support. *d*. Rod which communicates the movements of the spring to the lever *l*, and thus to the writing-needle *G*. *c*. Leaden tube by which the cavity of the spring is in communication with the artery.

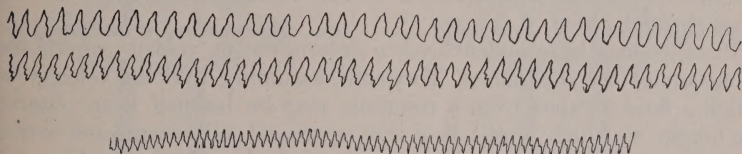
Admirable an instrument as the kymograph undoubtedly is, and however accurately it fulfils its purpose, it must not be forgotten that the trace recorded on the cylinder is due to the oscillations of the mercury, and, therefore, only indirectly to the pressure of the blood. On account, however, of the inertia of the mercury and the suddenness of the expansion of the artery, the oscillations of the mercury, though caused by the pressure of the blood, are not an exact measure of it, since by the time the mercury has risen to its highest elevation the artery has collapsed. If the heart is beating very quickly the extent of the oscillations of the mercury is relatively too small, and if the interval between the pulsations is prolonged the excursion of the manometer is too great. The use of the mercurial kymograph is, therefore, limited to the study of the mean pressure and of variations in pressure such as occur at sufficiently long intervals to prevent the oscillations being mixed up with those proper to the instrument. In order to study the variations of blood pressure in the exact order in which they occur, and as regards their duration and degree, etc., we make use of Fick's spring kymograph,



which is so constructed that it transmits the movements communicated to it without obscuring them by any movement of its own.

The instrument (Fig. 191) consists essentially of a hollow C-shaped thin metal spring (*a*) filled with alcohol and communicating through its proximal end (*b*) by means of a connecting tube (*c*) with the pressure bottle containing the solution of the sodium bicarbonate and the arterial canula. The proximal end of the spring being fixed, as the blood pressure increases the spring tends to straighten itself and the distal or free end makes the movements which follow exactly the variations in the arterial tension. These movements are most exact, the slightest variations in the blood pressure being expressed by them. As they are, however, very small before being recorded, they are enlarged by the lever which is carried by the distal end of the spring. It will be seen from Fig 192, illustrating a trace of the blood pressure in the carotid

FIG. 192.



Traces in rabbit taken with Fick's spring kymograph.

artery of the rabbit, taken by the spring kymograph, that the ascent of the lever, due to the expansion of the artery caused by the ventricular systole, is very abrupt, almost vertical, that at the vertex the direction of the trace is horizontal, that the lever in its descent pursues an oblique course at its termination, being also horizontal in direction, and that the dicrotism of the pulse is very evident. The nature of these peculiarities we have already considered in describing the pulse. If we wish to express in millimetres of mercury the absolute blood pressure determined by the spring kymograph, the instrument must first be graduated by comparison with a mercurial manometer. This is done in the following way: The spring kymograph being so placed that it will write on the recording cylinder, its connecting tube in communication with the pressure bottle is adapted to the proximal end of the mercurial manometer. The pressure bottle is first lowered until the solution it contains stands at the same level as that of the mercury in the manometer. The clockwork being put in motion the cylinder revolves and a trace is taken which will represent the abscissa. The pressure bottle is then raised till the mercury is elevated in the distal limb of the manometer 10 mm. ( $\frac{2}{3}$ th of an inch) higher than in the proximal one, and a second tracing taken, and so on until we have obtained a number of tracings parallel with the first one or abscissa, and therefore with each other. The vertical distance between the abscissa, and these lines or the ordinates measured in millimetres expresses then the value of the tracing in millimetres of mercurial pressure.

We have already alluded incidentally to the influence of respiration in modifying the curve of the blood pressure, and, as we have now seen, how

the latter may vary according to the part of the vascular system generally. It is probable, also, that the blood pressure depends, to a certain extent, upon the size of the animal, the period of life, and general health, *cæteris paribus*, the blood pressure being greater in larger than in smaller animals, in those of middle age than in very young or very old animals, in strong, healthy than in weak, sickly ones. Inasmuch as the pressure of the blood depends upon the muscular force of the heart, and as the muscular substance of the heart, like all other muscle, is nourished by the blood, it follows that loss of blood in weakening the fibre of the heart and the amount of blood expelled, should diminish blood pressure. The experiments of Hales<sup>1</sup> and Colin<sup>2</sup> have shown that such is the case, the blood pressure being diminished in proportion to the amount of blood lost. Finally, we shall see that the vasomotor nerves, in modifying the calibre of the vessels, greatly influence the bloodvessels. In concluding our account of the arteries, there still remains for us the consideration of the velocity with which the blood flows through them.

Physiologists have endeavored to determine the velocity of the blood by means of the theorem of Torricelli, assuming that the velocity with which a fluid escapes from a reservoir may be learned from observing the height to which it will flow into a vertical tube connected with the same, the velocity being equal to that which a body would acquire falling *in vacuo* through a distance equal to the height which the fluid attains in the tube, which is nearly the same as the level of the fluid in the reservoir. The velocity, however, that a body acquires while falling through a given height is expressed by the formula,  $V = \sqrt{2gh}$ , in which  $V$  is the velocity,  $h$  the height, and  $g$  the accelerating force of gravity. To obtain the velocity with which the blood flows from the heart into the aorta we must substitute, therefore, in the above formula for  $h$  the height to which the blood rises into a vertical tube inserted in the carotid artery, which, in the case of the horse, for example, has been found to be 3 metres (117 inches), and for  $g$ , or the accelerating force of gravity, 9.8 metres (32 feet), then  $V = \sqrt{2 \times 9.8 \times 3} = \sqrt{58.8} = 7.6$  metres—that is, the velocity would be about 7.6 metres, or about 24 feet in a second. Practical engineers, however, know that in hydrodynamic machines the velocity of the flow, on account of friction, etc., is rarely what theory teaches it ought to be. The physiologist has still less reason even to find much agreement between the results of theory and experiment as regards the velocity of the blood, as the perturbing causes, among which may be mentioned the resistance offered by the column of blood in the aorta, are so numerous. Indeed, little or no importance can be attached to this manner of investigating the velocity of the blood in the arteries. In fact, we will see that the velocity just given is a gross exaggeration.

Among the first to determine with anything like accuracy the velocity of the blood may be mentioned Hales, who, as we have already seen, studied the subject of blood-pressure with so much success. Assuming, according to well-known hydraulic principles, that the velocity with

<sup>1</sup> Statical Essays, vol. ii, p. 16. London, 1740.

<sup>2</sup> Milne Edwards: Physiologie, tome iv. p. 115.



which a fluid, in a given time, flows through a tube is equal to the ratio of the efflux to the sectional area of the tube, Hales estimated that the blood in the horse flows from the left ventricle into the aorta at the rate of nearly 17 inches in a second, which we will see agrees closely with the velocity recently determined by experiment. Hales' method of calculation is as follows. Assuming the capacity of the left ventricle to be 10 cubic inches, and the area of the transverse section of the aorta 1.036 inches, the ratio of these two quantities, or  $\frac{10}{1.036}$ , equals 9.65 inches, will be the column of blood that passes from the left ventricle into the aorta during each systole. Supposing that the heart beats 36 times in a minute, then  $9.65 \times 36$  equals 347.40 inches of blood, would pass from the heart into the aorta in a minute;

FIG. 193.

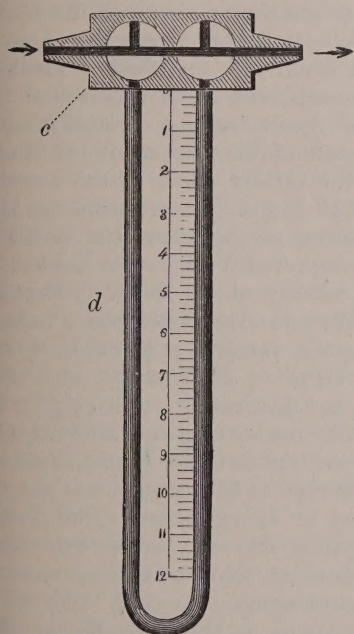
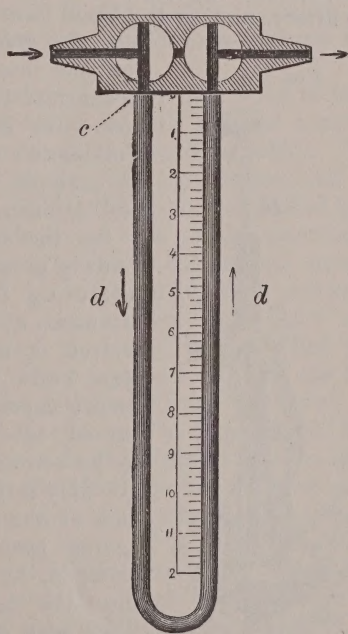


FIG. 194.



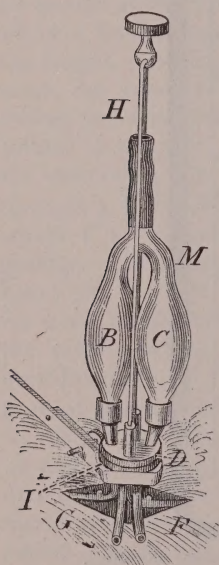
Volkmann's hæmodromometer for measuring the rapidity of the arterial circulation.

but as the ventricular systole lasts, according to Hales, only one-third (really four-tenths) of the period intervening between two cardiac beats, the velocity must be three times as great, or 1042.20 in a minute—that is,  $347.40 \times 3$  equals 1042.20 inches, or 86.85 feet; dividing this by 60, we obtain 1.4 foot, or 16.8 inches, for the velocity with which the blood flows from the heart into the aorta in a second. The first physiologist, as far as I know, who endeavored to determine, not what the velocity of the blood ought to be from theory, but what the velocity actually is in a living animal by experiment, was Volkmann.<sup>2</sup> The hæmodromometer, or the instrument

<sup>1</sup> Hæmostatics, vol. ii, p. 46.<sup>2</sup> Hæmodynamik, S. 185

which he invented for this purpose, consists of a metallic tube (*e*), which is united to the two ends of a divided artery, and through which the blood can flow in the same direction as through the vessel itself (Fig. 193). To the metallic tube is attached laterally a U-shaped glass tube (*d*), containing water. By turning stopcocks the metal tube is put in communication with the U-shaped tube in such a way (Fig. 194) that the blood cannot pass at once as it did before from the artery through the metal tube to the artery again, but must first pass through the U-shaped tube. The length of this tube being known, and the time it takes for the blood to flow through it being observed, the velocity with which the blood flows through the artery can be determined approximately. There are objections, however, to the use of this instrument, as the blood does not flow through the glass tube as easily as it does through the artery, both on account of the curvature of the tube and of the difference in its substance as compared with that of the artery, and as the blood flows from the proximal end of the artery

FIG. 195.



Ludwig's stromuhr.

into the glass tube it drives ahead the water it contains into the distal end, the effect of which is to contract the vessels, and so further retard the flow. It is for these reasons, probably, that Volkmann's estimate of the velocity of the blood, for example, in the carotid artery of the horse of 254 millimetres (10 inches) in a second is too low.

By the invention of the stromuhr, in 1857, Ludwig greatly improved Volkmann's method of measuring the velocity of the blood. This instrument, also called the rheometer (rheo, to flow, metron, a measure), consists (Fig. 195) of two glass bulbs (*B*, *C*) of an ovoid shape, and of a known capacity, communicating superiorly by the curved tube and terminating ~~so~~ inferiorly as to be screwed into the canulæ *F* and *G*, which are only large enough to be inserted into the cut ends of the artery to be examined. The canulæ having been ligated, and the vessel previously clamped, by means of the small tube opening into the communicating tube, the bulb *C* is filled with olive oil up to the mark *M*, the bulb *B* with serum. The small tube is then closed.

The clamps having been removed, the blood flows from the proximal end of the artery by means of the canula *F* into the bulb *C*, driving the oil ahead of it through the communicating tube into the bulb *B*, the serum in the latter being driven out of it through the canula *G* into the distal end of the artery. So far, the method of experimenting with the stromuhr is essentially the same as that of the hæmodromometer, with these two differences, however, that serum being used instead of water there is less resistance offered to the flow of the blood, and, on account of the shape of the bulbs, a greater quantity of blood can be used, which is also of advantage. The great improvement, however, in Ludwig's instrument, as compared with Volk-



mann's, consists in this, that by turning the vertical rod *H* through 180 degrees, by means of the mechanical arrangement to be explained in a moment, the bulb *B* now filled with oil, communicates through the canula *F* with the proximal end of the artery, and the bulb *C* filled with blood communicates through the canula *G* with the distal end. The blood still flowing from the proximal end of the artery will now drive the oil out of *B* into *C*, and the blood displaced by the oil will pass into the distal end. By turning the rod back again the bulb *C* will communicate with the canula *F*, and the bulb *B* with the canula *G*. This operation can be repeated several times before the blood coagulates. The mechanical arrangement, by which the bulbs *C* and *B* are alternately put in communication with the canulæ *F* and *G*, consists simply in fixing the inferior ends of the bulbs into the movable disk *D*, into which the vertical rod *H* is inserted, the canulæ *F* and *G* being fixed into the immovable disk *I*. When the movable disk *D* is in the position shown in Fig. 19~~E~~ then *C* communicates with *F*, and *B* with *G*; when the disk has been rotated through 180 degrees then *B* communicates with *F*, and *C* with *G*.

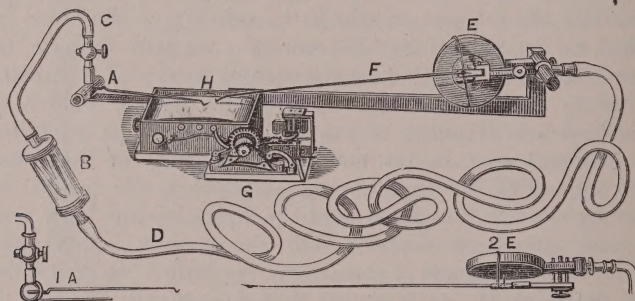
To illustrate the manner in which the velocity of the blood is determined in a living animal by the stromuhr we will suppose that the instrument has been adapted to the carotid artery of a rabbit. The animal having been firmly secured to the Czermak holder, and the artery exposed and clamped in two places, the clamps separated by a distance of about two inches and about an inch of the intervening vessel cut out. The stromuhr being attached to the vertical stem of the holder by the horizontal rod and the bulbs having been previously warmed and their ends screwed into the canulæ which have been inserted into the cut ends of the artery, the bulb *C* is then filled with oil up to the mark *M*, it containing then 5 c. cm. (2 in.), and the bulb *B* with serum. The clamps are now withdrawn from the artery and the blood from its proximal end will be observed to drive the oil from *C* into *B*, the oil displacing the serum in *B* which passes into the distal end of the artery. The moment that the blood reaches the level of the mark *M* the movable disk *D* is rotated as rapidly as possible through 180 degrees with the effect of putting the bulb *B* filled with oil in communication with the proximal end of the artery and the bulb *C* filled with blood in communication with the distal end of the vessel. The blood continuing to flow, the oil is now driven from *B* into *C*, the disk being rotated back again the moment that the blood reaches the level of the mark, the bulb *C*, now filled with oil, communicates as at first with the proximal end of the artery. The experiment may be continued in this way for a minute or more until the blood begins to coagulate. Inasmuch as we learn how often in a given time a definite quantity of oil is displaced by the blood we learn how much blood is delivered by the carotid artery in that time. Suppose, for example, that in an experiment 5 c. cm. (2 in.) of blood have been delivered by the carotid artery 10 times in 100 seconds—that is, 50 c. cm., then 1 c. cm. of blood has flown from the artery in 2 seconds, or 0.5 c. cm. equal to 500 mm. in 1 second. Dividing this amount by the sectional area of the artery through which it has flown—that is, by 3.14 mm., the diameter of the artery and the canulæ being nearly the same, or 2

mm., we get the velocity, or nearly 159 mm. (6 in.) in 1 second:  $\frac{500}{3.14}$  equals 159 mm., according to the hydraulic principle that the velocity equals the ratio of quantity to sectional area.

The stromuhr is a most excellent and reliable instrument, as it interferes so little with the circulation, the flow of the blood being only stopped during the instant that the disk is rotated and the blood pressure being little altered by its passage through the instrument. This can be shown by connecting a manometer with the two tubes which are in communication with the bulbs, but which are not seen in the illustration, the tubes being placed in the side of the apparatus not shown in the figure.

While the stromuhr is admirably adapted to determine the exact amount of blood passing through an artery and the mean velocity of the flow, it does not, however, enable us to determine the incessant variations experienced by the blood as regards its velocity. For this object we make use of the hæmodromometer of Chauveau.

FIG. 196.

Hæmodromograph of Chauveau and Lortet.<sup>1</sup> (McKENDRICK.)

The construction of this instrument, like the hæmatometer of Vierordt<sup>1</sup>, is based upon the principle of measuring the velocity of the blood by observing the amount of deviation undergone by a pendulum, the free end of which is suspended in the blood current, the amount of deviation being proportional to the velocity. It is essentially the same kind of instrument as the hydrostatic pendulum used by engineers to measure the velocity of a current of water. Chauveau's hæmodromometer, invented in 1858,<sup>2</sup> consists of a brass tube about 4 cm. (1½ in.) long (Fig. 196, A), which is inserted into the cut ends of a divided artery, or into the slit made in the vessel of the horse and ligated. Part of the wall of the tube is of India-rubber membrane fastened over a longitudinal opening in the tube, and through which passes a light lever 4 cm. long. The short expanded arm of the lever hangs freely in the blood, and is moved through a greater or less arc, according to the force with which the blood rushes against it, in from the artery, the India-rubber membrane acting as a fulcrum. The movements of the long arm of the lever H in the opposite direction to

<sup>1</sup> Die Erscheinungen und Gesetze der Stromgeschwindigkeit des Blutes, 1858.

<sup>2</sup> Journal de la Physiologie, tome iii. p. 695. Paris, 1860.



those of the short one are measured by means of a graduated scale. The long arm of the lever, it will be observed, projects considerably from the tube A. In order to determine the actual velocity of the flow in addition to the varying changes the instrument must be first experimentally graduated. This can be done in the following way: A current of warm water, or, better, defibrinated blood, is made to pass through the tube of the hæmodromometer with such a velocity that the deviation undergone by the pendulum is the same as when the instrument was inserted in the artery. The velocity of the current can be easily determined by receiving the fluid from the tube in a graduated vessel, and observing the time occupied in discharging a given quantity.

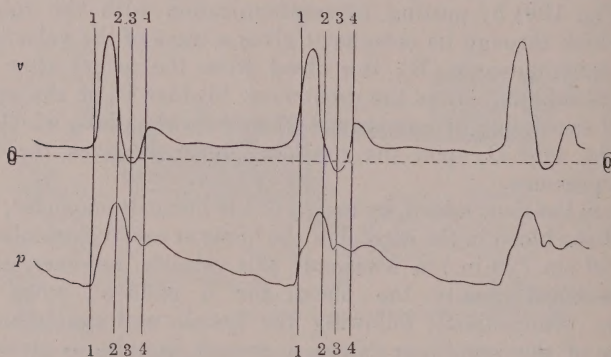
When a marker is attached to the end of the long lever H, the movements can then be recorded on the cylinder, and we obtain a graphic representation of the velocity and its variations. The hæmodromometer, when used in this way, becomes the hæmodromograph. Lortel has modified Chauveau's instrument so that a trace of the blood pressure can be taken simultaneously with that of the velocity. This is accomplished (Fig. 196) by putting in communication with the tube A the lever of which through its movement gives a trace of the velocity of the blood, a sphygmoscope (B), the blood from the artery after passing through the tube A, enters the caoutchouc bladder B, of the sphygmoscope, and expanding, it compresses the air in the glass, which, acting through the tube D, upon the recording lever F, gives the trace of the blood pressure.

Chauveau has determined, by means of his hæmodromometer, that the velocity of the blood in the carotid of the horse at each ventricular systole is about 50 cm. (20 in.) in a second; this velocity, however, gradually diminishes until finally the blood, for a moment, stops moving altogether. Immediately following the systole and synchronous with the closure of the semilunar valves, a second impulse is given to the blood by the recoil of the arterial walls, and the blood moves now at a rate of about 20 cm. (8 in.) a second; this velocity gradually diminishes, the average rate being, until the next ventricular systole, about 12 cm. (5 in.) in a second. It will be observed, from these experiments, that the velocity of the blood is at times much more rapid than at others. This is, however, only true of the arteries near the heart, like the carotid, the acceleration of the velocity, like the pulse, gradually disappearing in the small arteries, and for the same cause, the gradual diminution of the cardiac pressure, as we recede from the heart to the periphery. While the velocity of the blood in the arteries in man can be experimentally determined from the experiments made upon the horse, approximately, it may be considered as not differing very much from that observed in that animal. The velocity of the blood in the arterial system is not only modified, as we have seen by the cardiac pressure, but is influenced by other causes.

It has already been mentioned that the capacity of the arterial system increases as we pass from the aorta to the capillaries, and, as fluids move more slowly in the wide tubes than in narrow ones, the velocity of the blood ought to be slower in the peripheral arteries than in those near the heart. Experimentally, this has been shown to be the case; accord-

ing to Volkmann, the velocity of the blood in the metatarsal artery in the dog is only 5 cm. (2 inches), that of the carotid artery being 25 cm. (10 inches) in the second. The velocity of the blood will vary, also, according to the resistance offered to its flow; the compression of an artery, for example, offering an obstacle to the circulation, will diminish the velocity, and even stop the movement altogether. The amount of resistance offered by the capillaries greatly influences the velocity of the blood. The capillary resistance remaining constant, an increase in the force of the heart will increase the velocity; a diminution in the cardiac force will diminish it. On the other hand, the force of the heart remaining constant, the velocity of the blood will be either increased or diminished, <sup>inversely</sup> according as the capillary resistance is increased or diminished. It will be observed from what has been said in reference to the pressure of the blood and its velocity, that, with the increase or diminution of the one we have often a corresponding in-

FIG. 197.



Tracings of variations of rapidity and of pressure of blood in the carotid of a horse, obtained by Chauveau and Lortet. The line *v* represents the curve of the rapidity of the blood; and *p* the curve of arterial pressure. The figures and vertical lines represent corresponding periods in the tracings. (McKENDRICK.)

crease or diminution of the other. Thus, when the action of the heart is diminished by stimulation of the pneumogastric nerve, the velocity and blood pressure are diminished at the same time. The relation of the two, however, may be an inverse one—that is, the velocity may be diminished, and yet the blood pressure may be increased; for example, if an artery be compressed the velocity is diminished, and yet the blood pressure rises, as we have seen. As Marey expresses it, any influence which increases or diminishes the force of the heart, which propels the blood toward the periphery, will increase or diminish at the same time the velocity and blood pressure, as in the example just given of the effect of stimulation of the pneumogastric nerve; on the contrary, any influence which will increase or diminish the resistance to the arterial flow will make the velocity and blood pressure vary in the inverse relation toward each other. Thus, if the capillary resistance be very great the velocity is diminished but the blood pressure rises.

On account of this relation between the pressure of the blood and its



velocity, wherever it is practicable the two should be studied together (Fig. 197), since it is impossible to learn from the elevation of the mercury in the manometer alone whether the rise in the blood pressure is due to increased cardiac action, or increased peripheral resistance. If, however, the trace of the velocity be taken simultaneously with that of the blood pressure, and it is seen that the velocity is diminished, then the rise in the blood pressure will be due to peripheral resistance; on the other hand, if the velocity be increased, then it is due to increased heart action. The want of such comparative observation leaves us often in doubt as to what the rise in the blood pressure, as indicated by the elevation of the mercury, was really due to in many of the recorded experiments upon blood pressure. The result of Chauveau's observation upon the coronary arteries with his hæmodromograph illustrates the importance of this comparative method of experimentation. It being demonstrated that, during the systole of the ventricle, the velocity of the blood is diminished in the coronary arteries, the rise in the blood pressure observed must be due to peripheral resistance, the contracted state of the muscular substance of the heart during the systole offering an obstacle to the flow of the blood through the coronary arteries; the velocity being increased, however, during the diastole, and the blood pressure falling, shows that the obstacle has been removed, the muscular fibres of the heart now being relaxed. The above view is a confirmation of what has been already said in reference to the circulation of the blood through the substance of the heart itself.

## CHAPTER XXIII.

### THE CAPILLARIES.

THE capillaries, discovered by Malpighi, in 1661, are the minute vessels through which the blood (with few exceptions) flows from the arteries to the veins. As an artery becomes smaller and smaller it gradually loses its external and middle coat, and, to a great extent, its internal one also, the epithelial layer alone remaining. This constitutes a capillary. As the capillary approaches the vein it not only becomes larger, but changes the character of its structure, developing gradually three coats, until finally the capillary becomes a vein. Practically, it is impossible to say exactly where the artery ends and where the capillary begins, or where the capillary ends and the vein begins, the transition from one to the other is so gradual. It is for this reason that a difference of opinion prevails among anatomists as to what constitutes a capillary, and therefore the description of these vessels differs,

FIG. 198.



Capillary plexus in the portion of a web of a frog's foot, magnified 110 diameters. 1. Trunk of vein. 2, 2, 2. Its branches. 3, 3. Pigment cells. (CARPENTER.)

according to the view taken of their structure. According to some histologists there are various kinds of capillaries, differing from each other in the amount of muscular and fibro-elastic tissue present. Such vessels we would regard as either small arteries or veins, considering a capillary to be a transparent, apparently homogeneous, elastic vessel,

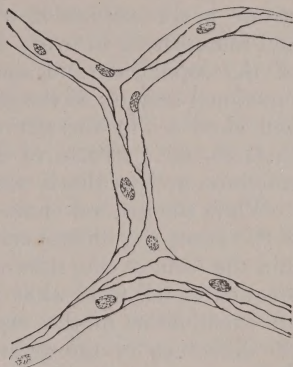


whose calibre is so small that the blood corpuscles can pass into it only one at a time (Fig. 198), and whose wall consists (Fig. 199) of a simple epithelial layer of flattened lanceolate cells, with oval nuclei, joined to edge, and continuous with the epithelial layer of the arteries on the one hand, and with that of the vein on the other. The wall of the capillary is apparently almost homogeneous, it is only after appropriate treatment with silver nitrate and carmine that the outlines of the cells composing it, with their nuclei, become apparent. The length of the capillary—that is, the distance between the end of the artery and the beginning of the vein—varies, on an average, between the  $\frac{1}{2}$  and  $\frac{1}{5}$ th of a mm. ( $\frac{1}{50}$ th and  $\frac{1}{125}$ th of an inch), the average diameter varying between the  $\frac{1}{80}$ th and the  $\frac{1}{140}$ th of a mm. ( $\frac{1}{2000}$ th and  $\frac{1}{3500}$ th of an inch). The smallest capillaries are found in the nervo-muscular tissues, retina, and patches of Peyer, having there a diameter of  $\frac{1}{160}$ th to the  $\frac{2}{40}$ th of a mm. ( $\frac{1}{4000}$ th to  $\frac{1}{6000}$ th of an inch); the largest in the glands and bones with a diameter of  $\frac{1}{80}$ th to the  $\frac{1}{120}$ th of a mm. ( $\frac{1}{2000}$  to  $\frac{1}{3000}$ th of an inch); the capillaries of the skin vary between these two extremes, having a diameter of from the  $\frac{1}{96}$ th to the  $\frac{1}{160}$ th of a mm. ( $\frac{1}{2400}$ th to  $\frac{1}{4000}$ th of an inch). The wall of the capillary varies between the  $\frac{1}{480}$ th to  $\frac{1}{1000}$ th of a mm. ( $\frac{1}{12000}$ th and  $\frac{1}{25000}$ th of an inch) in thickness.

After deducting this thickness, say the  $\frac{1}{12000}$ th of an inch, from the diameter, it will be observed that the calibre of the vessel is reduced to the  $\frac{1}{3000}$ th of an inch, so that the blood corpuscles can move only in a single row, and in many cases even the corpuscle must change its shape in order to pass into the vessel; this is possible through its elasticity.

The small size of the capillaries, both as regards their length and breadth, has an important significance in reference to the amount of blood flowing from them into the veins. Thus it is well known, from the researches of Poisseuille,<sup>1</sup> that the amount of fluid discharged by a tube the  $\frac{1}{100}$ th of a millimetre in diameter ( $\frac{1}{2500}$ th of an inch) will be sixteen times that discharged by a tube the  $\frac{1}{200}$ th of a mm. ( $\frac{1}{5000}$ th of an inch), the amounts discharged being proportional to the fourth powers of the diameters—that is,  $1 : x :: \frac{1}{200} : \frac{1}{100}$ , or  $x$  equals 2 and  $2^4$  equals 16. On the other hand, the amount discharged by tubes of the length of the capillaries will be inversely as their lengths—that is, of two capillaries of different lengths more fluid will be discharged from the short vessel than the long one. It will be seen, therefore, that any change in the length or breadth of a capillary will influence greatly the amount of blood delivered to the veins, and so increase or diminish the resistance offered by the capillary system to the arterial flow; the significance of which we have seen in considering the velocity of the

FIG. 199.

Fine capillaries from the mesentery.  
(CARPENTER)

<sup>1</sup> Mem. de l'Acad. des Sciences Savant Etrang, tome ix. p. 513.

blood and its pressure in the arteries. The cell-like structure of the capillaries just referred to makes perfectly clear how it is possible for the white and red corpuscles to pass from the capillary into the surrounding tissues. The capillaries, unlike the arteries and veins, constitute a true plexus of vessels of nearly uniform diameter, branching and inosculating in every direction. This inosculation is characteristic of the capillaries, and the plexus is developed in proportion to the functional activity of the part. Thus the capillaries are very numerous and close set in the nervo-muscular and glandular tissues, absorbing surfaces, etc., structures in which the molecular changes incident to nutrition are peculiarly active.

While the general character of the capillaries throughout the system is the same, the difference in their disposition as regards their closeness and the form of the network is often so marked that the histologist can frequently tell from what part of the body a tissue has been taken by an examination of the capillaries alone. No one can fail to recognize the difference in the arrangement of the capillaries in the skin (Fig. 200), as compared with that in muscle or mucous membrane (Figs. 201, 202). While capillaries are found almost everywhere in the human

FIG. 200.



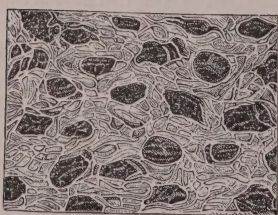
Distribution of capillaries on the surface of the skin of the finger. (CARPENTER.)

FIG. 201.



Distribution of capillaries in muscle. (CARPENTER.)

FIG. 202.



Distribution of capillaries around follicles of mucous membrane. (CARPENTER.)

body, it has been shown by Suquet<sup>1</sup> that in certain parts of the head and in the extremities the blood passes directly from the arteries into veins without the intervention of capillaries. Capillaries are absent in certain structures like cartilage, hair, nails, etc., and hence such parts are often called extravascular. This name is apt, however, to mislead and is inappropriate, since all tissues are extravascular in so far as they lie outside of the vessel carrying the blood that nourishes them. In the vascular tissues the nutriment osmose through the wall of the capillary into the tissue immediately surrounding the vessel and thence into parts more and more remote from it. In the so-called extravascular tissue the nutriment comes from the blood of a capillary, as in the vascular tissue, though the capillary may be situated at a considerable distance from the tissue that it nourishes. The only difference between the vascular and extravascular tissue is that the nutriment is conveyed

<sup>1</sup> De la Circulation du Sang dans les membres et dans la tête de l'Homme. Paris, 1860.



a longer distance in the one case than the other; the difference, therefore, is one of degree, not of kind. There are no capillaries in the spleen, erectile tissues, and maternal part of the placenta, their place being supplied by blood sinuses. When we come, however, to the study of the development of these organs, we shall see that these blood sinuses are probably enormously dilated capillaries. It will be remembered that the arterial system was likened to a cone, of which the heart is the apex and the capillaries the base, and that the area of the branches of an artery is usually greater than that of the artery itself. We should expect, therefore, to find that the capacity of the capillary system is far greater than that of the arterial. Indeed, the microscopical examination of the skin, mucous membrane, muscle, etc., in which the capillary vessels have been injected gives the impression that such tissues consist of nothing but capillaries. This is also true almost to the same extent in living animals under certain conditions, thus during digestion the surface of the mucous membrane lining the alimentary canal presents a light red appearance through the distention of its capillaries with blood.

The capacity of the capillary system must be immense—indeed, according to Vierordt,<sup>1</sup> it is 800 times that of the arterial. This estimate, though only approximative, cannot be very far from the truth, being deduced from the law that the velocity with which a fluid flows through a tube is inversely as the diameter of the tube. We shall soon see, as an illustration of this law, that the blood flows much more slowly in the capillaries than in the aorta, the total area of the capillaries being far greater than that of the aorta. The sectional area of the capillary system being then to the sectional area of the aorta as the velocity of the blood in the aorta is to the velocity of the blood in the capillaries, the

$$\text{sec. area of capillaries} = \frac{\text{sec. area of aorta} \times \text{vel. of blood in aorta}}{\text{vel. of blood in capillaries}}.$$

Donders's<sup>2</sup> estimate of the capillary system being 500 times that of the arterial—rather too low—is based upon the observations of Volkmann.

By dividing the total sectional area of the capillaries by the area of one capillary an approximate estimate of the number of capillaries can be obtained. It was in this way that Hales<sup>3</sup> calculated that there were over eight millions of capillaries in the human body. The general structure, distribution, etc., of the capillaries having been described, let us now consider the manner in which the blood flows through them.

As the phenomenon of the flow of the blood through the capillaries, as viewed by the microscope, is one of the most beautiful and striking spectacles in nature, a few words as to the most convenient method by which it can be observed appear necessary. For this purpose we generally make use of the mesentery of the frog, on account of it being so easily exposed and readily arranged on the apparatus supporting it, which is a very simple one, consisting of a thin piece of cork with an opening in it through which the light can pass, and upon which rests, slightly elevated, a glass slide, over which is placed the mesentery, the

<sup>1</sup> Die Erscheinungen und Gesetze der Stromgeschwindigkeiten des Blutes, S. 35.

<sup>2</sup> Physiologie, Band i. S. 131.

<sup>3</sup> Statistical Essays, vol. ii. p. 69.

loop of intestine drawn out of the body to which the mesentery is attached resting in a little gutter or groove on the glass slide surrounding the opening. A few drops of a solution of sodium chloride (3 per cent.) being placed upon the mesentery and a slide cover placed over it, and the cork placed on the stage of the microscope, the circulation can be observed for a considerable time before inflammation sets <sup>in</sup> up. The web of the frog's foot, its lung and tongue, may also be used for the demonstration of the circulation. The tongue of the frog, on account of its being attached to the anterior part of the lower jaw and free posteriorly, and therefore being easily drawn out of the mouth and through its great vascularity, is also a favorite subject of study with physiologists. When the tongue is used it is best, however, to inflate it first and then slit it open, when a magnificent view of the circulation is obtained. The tail of tadpoles, of little fish, and the gills of the salamander, are also serviceable objects for the study of the circulation. When the salamander is used it should be placed in a Holman's life slide, by means of which the animal is firmly secured without injuring it, while the water is constantly renewed. When the fish is used, Caton's fish-trough will be found serviceable. This consists of an oblong box, one end of which transmits the light through an opening in the piece of glass upon which the tail of the fish in which the capillaries are to be examined is secured, the head and body of the fish resting at the other end of the box. By means of a cistern and tube, a constant current of water passes through the box.

The study of the capillary circulation in mammals is more difficult than in any of the animals just referred to, since, with the exception of the wing of the bat, there is no external part transparent enough to be observed with the high power of the microscope, and if any of the internal parts are used the effects of exposure are far more injurious than in the frog, for example. The mesentery and omentum of small rodents, like rats and mice, etc., have been often made use of in demonstrating the capillary circulation in the mammalia; but the omentum of the guinea-pig is preferable for many reasons, on account of its transparency and of its delicate and simple structure, consisting, to a great extent, of only two layers, of being attached to only one side of the stomach, and little or no fat being present. The great difficulty experienced in observing the capillaries in the peritoneum of the mammalia is due to the injurious effects of exposing the membrane to the atmosphere and the risk of wounding it. To avoid this, the omentum, which is the part we shall use, is floated into a glass trough containing either serum or a solution of sodium chloride (3 per cent.), which is kept at the temperature of the body by means of the warm stage, which we have already described. The guinea-pig used should be put under the influence of chloral, three grains injected under the skin being sufficient for an animal weighing one pound, and then placed upon a support on a level with the stage of the microscope. The incision being made a little below the ensiform cartilage, and extending outward from the rectus muscle, about an inch from the edge of the omentum is carefully seized and drawn out into the trough. It is well to cover the parts of the membrane not immediately under the microscope with pieces of blotting-paper, in this way



avoiding unnecessary exposure, and at the same time keeping the omentum steadier than it otherwise would be. With all the above precautions, however, the view of the capillary circulation thus obtained is far from satisfactory, and not comparable to that observed in the mesentery of the frog.

Since the time of Malpighi, the phenomena of the capillary circulation have been often described; but language is inadequate to give one any idea of the beauty of the spectacle, and to be appreciated it must be seen.

We will suppose the mesentery of the frog disposed within the field of the microscope as just described. Here may be seen the arterioles of the mesenteric artery through which the blood flows with apparently amazing rapidity, dividing and subdividing until the blood is carried to an exquisite network of delicate tubes resembling a web of fine spun glass, the capillaries, in which the blood is separated from the tissues by a thickness varying between the  $\frac{1}{25}$ th and the  $\frac{1}{50}$ th of a mm. ( $\frac{1}{12000}$ th and  $\frac{1}{25000}$ th of an inch) only.

It will be readily appreciated, therefore, with what rapidity the nutritive elements can osmose into the tissues and the effete matters be taken up by the blood. Indeed, the capillaries are the seat of all physiological and pathological nutrition processes. The arteries and veins are only means toward an end, the one set of vessels carrying the blood to the part to be nourished, the other carrying it away laden with the waste products. It will be observed that the true capillaries are of uniform diameter, and are so small that they admit but a single row of corpuscles, and these are seen moving in the middle of the stream, flowing along in the clear plasma which forms a distinct layer, and which adheres to such an extent to the walls of the capillary that it appears immovable, and for this reason is called the still layer. The presence of this still layer is due to the capillary attraction existing between the liquor sanguinis and the wall of the capillary, and in proportion as the diameter of the capillary is diminished this force is relatively increased, since a greater surface of the capillary wall is exposed to the liquor sanguinis; there being little or no affinity between the red blood-corpuscles and the wall of the capillary, the corpuscles meeting with no obstacle to their flow consequently move with great rapidity through the middle of the stream. A red corpuscle is sometimes caught in the still layer, where it moves slowly for a time, turning over and over; sooner or later, however, it passes again with the central stream and in an instant is whirled out of sight. The white corpuscles, on the contrary, through their adhesiveness, stick either to the still layer or to the capillary wall, and being quite numerous in the frog (1 white to 8 red) a number are often seen at one time in the same capillary.

It is an interesting illustration of the uniformity of the laws of nature that the same phenomenon of the rapidity of the flow of a stream being greater in the middle than at the sides is seen on a magnificent scale in the motion of a glacier. It has been a matter of daily observation to those passing any time on a glacier to notice that the stones, débris, etc., move more rapidly in the middle of the glacier than those at the sides. It was Poisseuille<sup>1</sup> who first showed that the law regulating the flow of

<sup>1</sup> Recherches sur la cause du Mouvement du Sang dans les vaisseaux capillaires.

liquids in tubes was applicable to such having as small a diameter as those of the capillaries. The corpuscles often move in such a manner that they appear as if they were endowed with consciousness and volition. Thus when the single rows of corpuscles flowing in two capillaries reach a third vessel, formed through the union of the other two and only large enough to admit one row, one row will hold back until the other one has passed into the capillary and then will follow in its turn. Frequently the corpuscles will flow in one direction and meeting some obstacle will entirely reverse their course. A corpuscle is often retarded for some time by the angle formed by the division of a capillary into two, and may be observed turning over and over and changing its shape according to the pressure of the current until it is swept finally into the main stream.

Certain capillaries will be for a time quite empty, while others near by are filled with corpuscles, then one or two corpuscles will float into the empty capillary, in a moment or so a few more, and soon a current is established, while in the same gradual way a distended capillary may become empty. One of the most striking facts in the phenomena of the capillary circulation is the uniformity with which the blood flows through these vessels. The motion is here perfectly continuous; we no longer observe either the intermittent or remittent action so characteristic of the heart and arteries. We observe that the flow of the blood in the capillaries is never the same for any length of time—indeed, one of its most interesting peculiarities is the constant manner in which the scene varies—influenced as it is by so many conditions. In endeavoring to follow the course of the corpuscles as they flow through the capillaries, one's first impression, seeing them often swept along as if in a torrent, is that the velocity of the flow must be very great. Reflection at once suggests to us, however, that in proportion to the power of the microscope used the velocity is magnified. According to Milne Edwards,<sup>1</sup> Hales was the first who endeavored to determine by observation the velocity of the blood in the capillaries. Hales<sup>2</sup> does not tell us, however, the manner in which he accomplished this, simply stating that on comparing the different velocities of the blood in the muscles and in the lungs of a frog, he found that the blood moves in the parallel cylindrical arteries in the straight muscles of its abdomen at the rate of one-tenth of an inch in nine seconds of time—that is, at the rate of an inch in ninety seconds or one minute and a half. The simplest way of determining the velocity of the blood in the capillaries is to substitute for the ordinary eye-piece of the microscope an ocular micrometer, and with a reliable watch held close to the ear to determine the time that it takes a blood corpuscle to pass across the field of the microscope, or the interval of space included between two or more divisions of the micrometer. Weber<sup>3</sup> was the first, we believe, to make use of this method. It was in this way that he determined the velocity of the blood in the capillaries of the tail of the tadpole to be about the  $\frac{1}{2}$  of millimetre in a second (the  $\frac{1}{50}$ th of an inch). Valentin<sup>4</sup> estimated the velocity in the

<sup>1</sup> Physiologie, tome iv. p. 286.

<sup>3</sup> Muller's Archiv, 1838, S. 467.

<sup>2</sup> Op. cit., vol. ii. p. 66.

<sup>4</sup> Physiologie, Band i. S. 482.



capillaries of the web of the frog's foot was about the same—in round numbers, about 2.5 cm. (one inch) in a minute. According to Volkmann,<sup>1</sup> the velocity of the blood in the capillaries of the gills of the tadpole is  $\frac{1}{5}$ th of a mm., in the tail of a little fish  $\frac{1}{10}$ th of a mm., and in the capillaries of the mesentery of a dog  $\frac{8}{10}$ th of a millimetre in a second—in round numbers, about 5 cm. (2 inches) in a minute.

Vierordt<sup>2</sup> makes use of an apparatus for measuring the velocity of the blood in the capillaries, which is based upon the fact that a body moving at a certain rate and illuminated but for a very short instant appears immovable. By placing between the mirror of the microscope and the object-glass a movable disk pierced with holes through which the light is transmitted, the object viewed is only seen when one of the holes passes across the axis of vision. If the length of time the blood corpuscle is illuminated be known and the blood corpuscle appear immovable, then the rate at which it is moving can be inferred. This physiologist has also calculated the velocity of the blood in the capillaries of the human retina. As is well known, the eye after a time becomes fatigued when exposed to a strong white light; if the eye be now compressed, one sees the image of a current in the form of a network. This appears to be due to the passage of the blood corpuscles through the capillaries of the retina. By calculating the space passed over in a given time by the image, Vierordt<sup>3</sup> estimates the velocity in this situation to vary between the  $\frac{6}{10}$ th and  $\frac{9}{10}$ th of a millimetre in a second. Assuming that the rapidity of the motion of the white corpuscles can be accepted as a means of estimating the velocity of the still layer, it can be stated that on an average the latter moves 9 to 17 times more slowly than the current in the middle. Inasmuch as the amount of blood required by the tissues varies very much from time to time, we should expect to find also great variations in the state of the capillaries in this respect. Thus at one time the capillaries supplying a tissue may be entirely empty or almost so, at another gorged with blood. It becomes important, therefore, to study the effects of such agents as will modify the calibre of these vessels or accelerate or retard the flow of the blood through them.

Among the most important of these may be mentioned the effects of cold, heat, electricity, certain local irritants, and changes in the physical and chemical composition of the blood. Thus a low temperature diminishes the quantity of blood in the capillaries and retards the circulation, while a high temperature, on the contrary, increases the amount and accelerates its velocity. The effect of cold upon the capillary circulation can be readily demonstrated by placing a piece of ice upon the part examined, the web of a frog's foot, for example, or the mesentery. The circulation will at once be observed to become much slower, stagnate, and often cease entirely, the capillaries are emptied and the small arterioles, those carrying usually two or three rows of blood corpuscles, will now admit only one row. If the ice be removed, the circulation will become normal again. If now the part examined be covered with water,

<sup>1</sup> Die Hæmodynamik, S. 184.

<sup>3</sup> Op. cit., S. 112.

<sup>2</sup> Op. cit., S. 35.

say at a temperature of  $40^{\circ}$  C. ( $104^{\circ}$  F.) or placed upon the warm stage at the same temperature, the quantity of blood in the capillaries will be greatly increased and the velocity so much accelerated, that it is with difficulty the corpuscles can be distinguished. The circulation can be at once arrested by the stimulus of electrical currents, the greatest effect being obtained when individual currents are used. The effect of the application of a local irritant, like a solution of common salt, when applied to the arterioles, and possibly also to the true capillaries, is at first to produce a constriction and a diminution in the velocity of the current. The constriction is, however, soon followed by a dilatation and the velocity is accelerated. This condition, however, lasts but a moment, an oscillation of the current begins, the velocity is diminished again, stagnation follows, the capillary becomes gorged with blood, the white corpuscles increase in number, and an inflammatory state is set up.<sup>1</sup>

Since the experiments of Poisseuille, it is well known that the composition of a fluid will influence the rapidity with which it flows through tubes of small diameter. Thus, solutions of potassium iodide and bromide, etc., flow more rapidly than solutions of sodium, calcium, and magnesium chloride, of sodium phosphate and carbonate. One would naturally infer then that the presence or absence of certain salts in the blood would influence the rapidity with which it flows in the capillaries. Such was experimentally proven to be the case by Poisseuille,<sup>2</sup> the rapidity of the circulation in the horse being diminished by the introduction into the blood of ammonium acetate and sodium chloride. The influence of respiration upon the capillary circulation will be considered when the subject of asphyxia is taken up; while the effect of the vasomotor nerves in modifying the calibre of the arteries, and thereby affecting the quantity of the blood delivered to the capillaries, will be deferred until we study the nervous system.

In speaking of the effect of irritants when applied to the capillaries, it was just stated that a constriction of the arterioles, and probably also of the capillaries, was the first effect. It has long been, however, a subject of discussion as to whether the capillaries are really contractile in the same sense as the arteries. It is possible that the cause of the difference of opinion that still prevails in reference to this matter, may be due to the fact of one physiologist regarding as a capillary what another would consider an arteriole. The arterioles are, undoubtedly, contractile, their walls containing muscular fibres, and since the layer of nucleated cells of which the capillary wall consists is continuous with the contractile tunic of the arteriole, the capillary may possess true contractility. This seems to be the case, at least in the capillaries of the embryo, as shown by Rouget,<sup>3</sup> where the nuclei of the cells stand out through the contraction of the capillaries. On the other hand, the diminution in the calibre of the capillary, often supposed to be an evidence of its contractility, is really due to a diminution in the pressure of the blood, the wall of the capillary recoiling upon its contents through its elasticity, from a previous state of distention.

<sup>1</sup> Thompson : Lectures on Inflammation, Edinburgh, 1813. Wilson Philip : Med. Chir. Trans., 1823, vol. xii. Wharton Jones : Guy's Hospital Reports.

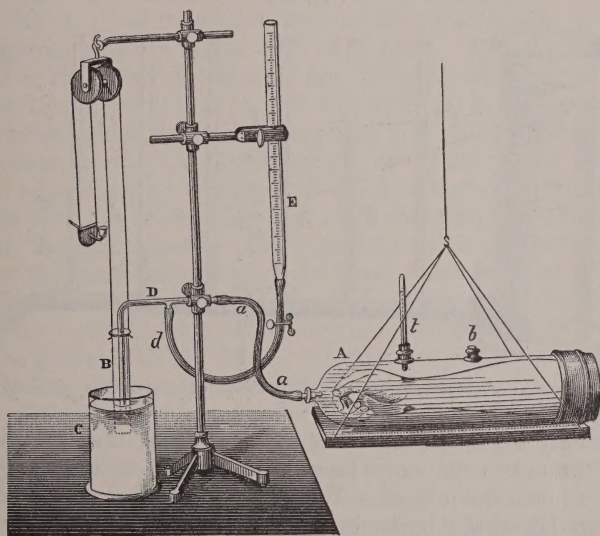
<sup>2</sup> Comptes Rendus de l'Acad. des Sciences, 1843, tome xvi. p. 60.

<sup>3</sup> Ibid., 1879.



When a tissue which has been thoroughly injected, is seen under the microscope, it appears as if it consisted almost entirely of capillaries. It will be readily understood that any change, however slight, in the calibre of the capillaries will considerably influence the volume of the organ containing them. The changes in the volume of an organ will serve then as a measure of the amount of the contraction and relaxation of its capillaries. Physiology is indebted to Mosso<sup>1</sup> more particularly for the employment of this method as a means of determining changes in the volume of the capillaries. For example, an isolated kidney in which the circulation is maintained artificially, is placed in a vessel filled with oil, the latter communicates with a second vessel. With an increase in the pressure, the volume of the kidney expands, and the oil is driven out of the vessel, with a diminution of the pressure, the organ contracts, and the oil is drawn back. The pléthysmograph of Mosso<sup>2</sup> is an instrument based upon the principle of the experiment

FIG. 203.



Pléthysmograph of Mosso. (MAREY.)

just described, having for its object the measurement of slow volumetric variations in the capillaries of man, depending upon either changes in the blood pressure, or variations in the state of contraction or relaxation in the vessels themselves. It consists essentially of a large glass jar (A, Fig. 203), in which an arm is enclosed, for example, and communicating by a tube with a small glass jar (B), which is suspended in the water of the jar C by means of the pulley and weight. The jar A enclosing the arm is filled with water. With each increase in the volume of the arm the water is driven out of the jar A through the tube into the jar B, sinking it deeper in the water of the jar C. With

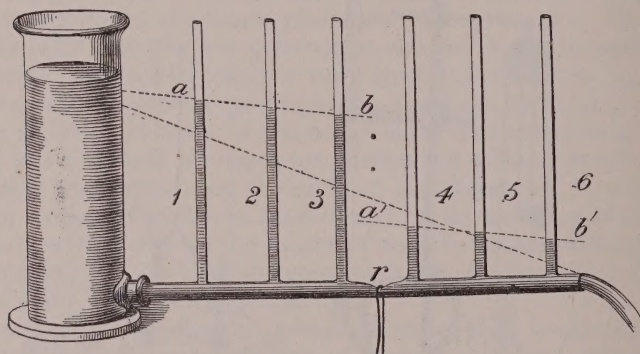
<sup>1</sup> Sopra alcune nuove proprietà delle pareti dei vasi sanguigni, *Recherche di fisiologia*, etc. Torino, 1875.

<sup>2</sup> Reale: Acad. delle scienze di Torino, xi., 1875.

each diminution in the volume of the arm, the water is drawn back into the jar A, the jar rising out of the water in C. A pen adapted to the weight, records graphically upon a cylinder the elevation and depression of the jar B—that is, the changes in the volume of the arm examined. From the results of his experiments, Mosso concludes that the changes in the volume of an organ are due not only to variations in the blood pressure, but also to changes in the calibre of the vessels as well.

It will be remembered, that in speaking of the pressure of the blood in the arteries, an experiment was performed, by which it was shown that the pressure of a fluid gradually diminished as it receded from the source of the supply to the outlet, the diminution being shown by the different heights to which the fluid rose in the vertical tubes. Let us now see what takes place when the fluid flows out of the apparatus (Fig 204), which is almost the same as that just referred to, with the

FIG. 204.



Apparatus to show decrease of pressure in tubes of unequal calibre. (MAREY.)

difference only that the diameter of the horizontal tube instead of being the same throughout its entire length, for a short distance in the middle (*r*), is very much diminished. We will consider this part as representing the capillaries, the horizontal portion of the tube on the left, the arteries, that on the right, the veins. It will be observed, as in the previous experiment, that the pressure diminishes very gradually and regularly in the tubes 1, 2, 3, corresponding to the arterial system, but that the pressure in the tubes 4, 5, 6, representing the veins, is very low, the blood passing from the arteries into the capillaries with difficulty, but readily passing out of the capillaries into the veins. Indeed, in the living animal at times, while the arterial pressure amounts to 150 to 200 mm. of mercury, the venous pressure is almost nothing. Such a difference in the pressure implies that the capillary offers great obstacles to the flow of the arterial blood. We have just seen that the adhesiveness between the liquor sanguinis and the walls of the vessels is so great as to give rise to the "still layer," and so retard the flow of a great portion of the blood, and the presence of this still layer must affect, to a



certain extent, the flow of the rest of the blood as well. Let us modify now the experiment a little, by substituting a somewhat larger tube for the one representing the capillaries in the last experiment. The effect of this dilatation of the capillary, it will be observed, is that the pressure in the artery, and in the arterial end of the capillary, is diminished, while the pressure in the venous end of the capillary, and in the veins, is increased. Any influence, therefore, that favors the retention of the blood in the arteries, will diminish the quantity of blood in the veins, and *vice versâ*.<sup>1</sup> The dotted line (Fig. 204) represents the effect of substituting the large tube.

Hales was the first, so far as I have been able to learn, who endeavored to determine the pressure of the blood in the capillaries. His method<sup>2</sup> of calculating this was as follows: Assuming the diameter of a capillary to be double that of a red corpuscle, "viz.,  $\frac{1}{1620}$ th part of an inch, or 0.000617; the periphery, therefore, of this vessel will be 0.000939, and its area 0.000000298; which, multiplied by 80, the number of inches to which the blood rose in the tube when fixed to the artery of the dog No. 1, gives 0.000239 part of 80 cubic inches of blood, or 21416 grains, equal to 0.515 part of a grain. But the resistance of the blood in the veins of the same dog being found equal to six inches height, or  $\frac{1}{13.33}$ d, or 0.075 part of 80 inches, this  $\frac{1}{13.33}$ d part equals 0.03039 grain, which being deducted from 0.5118 grain, the remainder, 0.4737 grain, is the force with which the blood would be impelled into such a capillary by a column of blood of eighty inches height."

It is an everyday observation that when one compresses the skin with the finger, the part becomes pale, regaining its natural color, however, as soon as the compression ceases, the blood returning then to the capillaries. In order that the blood should be driven out of the vessels of the skin, the external compression force must be superior to the internal one, or the pressure of the blood. If we know the amount of compression used, then we can estimate approximately the internal force, or the pressure of the blood in the capillaries. By means of a piece of glass, through which any changes in the color of the skin can be observed, and by gradually placing weights upon it, so that the amount of pressure used could be learned, Kries<sup>3</sup> has endeavored to calculate the pressure of the blood in the capillaries of a given surface. In this experiment, however, no account is taken of the resistance to be overcome otherwise than that of the blood. More recently, Roy<sup>4</sup> and Brown have used an apparatus for determining the pressure of the blood in the capillaries, which consists essentially of a cylinder closed inferiorly by glass, and superiorly by a transparent membrane covered with glass, which is placed within the field of the microscope. The air in the cylinder being compressed by a connecting tube, the membrane is pressed against the tissue containing the capillaries to be examined. As the compression is increased the circulation disappears in the capillaries, veins, and arteries. It would seem from the results of this kind of investigation that it is impossible to assign any absolute value to the

<sup>1</sup> Marey, op. cit., p. 357.

<sup>3</sup> Ludwig's Arbeiten. Leipzig, 1875.

<sup>2</sup> Op. cit., vol. ii. p. 55.

<sup>4</sup> Journal of Physiology, 1880, vol. ii. p. 223.

pressure of the blood in the capillaries, but that the pressure varies according to the volume of the capillaries.

While there can be no doubt that the heart is the main cause of the circulation, there are also good reasons for believing that there are other conditions than the contractile force of the heart and the arteries which influence the flow of the blood through the capillaries. As is well known, in plants, and in many of the lower animals, the nutrient fluid is carried to all parts of the system in the absence of a heart; analogy would lead us to expect, therefore, that there must exist in the higher animals a similar force, a capillary power, so to speak, which may be masked by the influence of a centralized powerful heart. This so-called capillary force appears to be inseparably connected with the nutritive and secretory processes, since what increases or diminishes the one influences in the same way the other. The idea of such a force is not a new one, it is embodied in the ancient aphorism of *Ubi stimulus ibi fluxus*. That some such power exists in the capillaries of the higher animals, independent of the action of the heart, is shown by the fact that the blood will still continue to flow in the capillaries after the heart has ceased beating, while, on the other hand, the heart may still be acting, and yet the circulation will entirely cease in the capillaries of certain parts. Local variations in the volume of the blood flowing through the capillaries, the reversal of the current in the vessels, changes in their diameter, so often observed in the healthy living animal, cannot be attributed to the action of the heart, but are evidently due to an influence engendered in the walls of the capillaries themselves, or in the surrounding tissues.

Many pathological facts might be mentioned as illustrations of such local variations. Thus, in cases of spontaneous gangrene of the lower extremities, although the heart may be beating, and the arteries and the capillaries entirely pervious, nevertheless the blood will not flow through the capillaries, the stopping of the circulation being due to a difference in the capillaries themselves, and the surrounding tissues. Again, it has often been demonstrated, at least in cold-blooded animals, that the flow of blood through the capillaries will continue even after the heart has been completely excised. While this cannot be shown experimentally upon a hot-blooded animal, the shock experienced being so great from so severe an operation, nevertheless nature often does in a gradual way what we cannot show by experiment. Thus, as is well known, after the general death of the body, urine has flowed from the ureters, sweat exuded from the skin, and glands have secreted. Such phenomena can only be explained on the supposition that the blood has continued to flow through the capillaries after the heart has ceased to beat. It is well known, since the observations of Dr. Bennett Dowler<sup>1</sup> upon the bodies of individuals who have died of yellow fever, that the veins often become so distended with blood within a few minutes after death that when opened the blood will spurt from them a foot or more. The tonicities of the arteries can hardly be supposed to account for this venous jet, or for the empty condition in which the arteries are almost always found

<sup>1</sup> Researches on the Capillary Circulation, New Orleans Med. and Surg. Journal, 1849.



after death—but to some additional force in the capillaries themselves. Further, we shall see, when we come to study the development of the circulation in the embryo, that the blood begins to move first in the *area vasculosa*, that is, toward the heart, not from it, and that the heart itself consists of cells so loosely attached together that it can be scarcely supposed to contract with force enough to account for the primitive circulation. Indeed, in the case of twins, it has been noticed that the heart in one of the two has even never been developed during the whole period of embryonic life, and yet the greater part of the organs were well formed. It might be supposed that the circulation in the twin in which the heart was absent was maintained by the heart of the one in which it was present, the blood from the one twin passing to the other through the vessels of the placentas, which were more or less in contact. This was shown by Dr. Houston<sup>1</sup> to be impossible, at least in the case reported by him.

In this connection the researches of Hyrtl<sup>2</sup> are interesting, this eminent anatomist having shown that the placental vessels do not communicate in those cases where the twins are of the opposite sex. The facts of comparative anatomy, experiment, pathology, embryology, all harmonize in showing that there exists in the capillaries some force independent of the heart's action, which aids the flow of the blood through them. It has often been supposed that the contractility of the capillaries aids the flow of blood through them. Admitting that the capillaries are contractile, this force could only be exerted in a rhythmical manner by alternate contractions and dilatations, a kind of peristalsis; but no such movement is observed, the blood flowing through the capillaries as if they were glass tubes. Further, it can be experimentally demonstrated that a diminution in the diameter of the capillaries, whether it be due to true contractility, or simply to elasticity, retards the flow of the blood, the blood pressure rising. The capillary force cannot, therefore, be of such a kind. On the other hand, the experiments of Weber and Wharton Jones have shown that electrical and chemical stimuli modify the capillary circulation, retarding the flow of the blood, and even producing complete stagnation, and yet no alterations in the diameter of the capillaries are observed, the change being evidently of a physico-chemical nature. Such facts, as well as those already referred to, show that there exists some mutual relation between the blood, on the one hand, and the walls of the capillaries and the surrounding tissues on the other.

It appears, then, that while the heart forces the blood into and through the capillaries, the rate at which it flows through these vessels will depend upon the general nutritive condition of the parts supplied by the capillaries, and that this capillary force can, under certain conditions, maintain the circulation independently of the heart.

Prof. Draper<sup>3</sup> suggests that the capillary force just referred to, may be of the same character as the force of capillary attraction, illustrating this view by the following experiment: "if two liquids communicating

<sup>1</sup> Dublin Medical Journal, 1837.

<sup>2</sup> Die Blutegefäße der Menschlichen Nachgeburt. Wien, 1870.

<sup>3</sup> Treatise on the Forces which produce the Organization of Plants, pp. 22, 41. Physiology, 1878, p. 131.

with one another in a capillary tube, or in a porous structure, have for that tube or structure different chemical affinities, movements will ensue, that liquid which has the most energetic affinity will move with the greatest velocity, and may even drive the other liquid before it." Thus, it will be noticed that if a capillary tube, containing gum, be immersed in a vessel filled with water, ~~that~~ the gum will rise in the tube, being displaced by the water, the water having a greater affinity for the walls of the tube than the gum. These experimental conditions are realized in the living body, the fresh arterial blood, on account of its oxygen and other nutritive elements having a greater affinity for the tissues than the effete venous blood, hence the arterial blood will push forward the venous blood from the systemic capillaries toward the veins. On the other hand, in the pulmonary capillaries just the reverse obtains, the venous blood drives forward the arterial, since the former has a greater affinity for the inspired oxygen than the latter, in which the blood is already oxygenated. According to the same physical principle, the portal blood, containing the same elements out of which the bile is elaborated, having a greater attraction for the hepatic cells than the blood of the hepatic vein, the latter will be driven out of the hepatic capillaries into the hepatic veins. Indeed, there must be a continual movement going on in every part of the economy, each cell having a greater attraction for the blood containing its nourishment than for that blood which has nourished it. Such a movement undoubtedly supplements the force of the heart.

The consideration of the influence of the nervous system upon the capillary circulation, whether as modifying through the vasomotor nerves the calibre of the arteries, or acting directly by changing the nutrition of the parts, will be deferred for the present. In concluding our account of the circulation of the blood it remains for us now to describe the flow of the blood from the capillaries back to the heart through the veins.



## CHAPTER XXIV.

### THE VEINS.

IN observing the flow of the blood through the capillaries, it will be seen that these vessels gradually pass into larger ones, the venous radicles, which in turn transmit the blood to the veins, the latter gradually uniting form two large trunks, the *venæ cavæ*, which, together with the coronary vein, transmit the blood to the right side of the heart and the pulmonary veins return it to the left.

The venous system may be regarded as consisting of two sets of veins, a superficial set returning the blood from the skin and surface generally, and a deep set which accompanies the arteries.

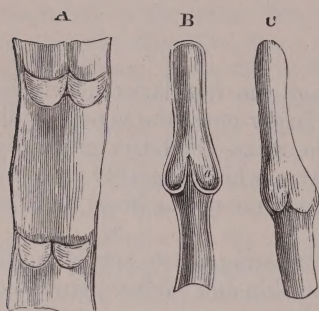
The veins differ in their structure from the arteries rather in degree than in kind, consisting essentially like the latter of three coats, an internal epithelial, a middle elastic muscular, and an external fibrous. The internal coat, consisting of subepithelial and elastic layers, is a continuation of the capillary, which we have seen is a prolongation of the internal coat of the artery. Indeed, it is practically impossible to say exactly where the artery ends and the capillary begins, or where the capillary ends and the vein begins, the transition from the one set of vessels to the other is so gradual.

The middle coat, containing the *vasa vasorum*, consists principally of fibrous tissue disposed in a longitudinal direction with some elastic fibres, and of a circular coat of elastic and muscular fibres mingled with some fibrous tissue. The external coat, like that of the artery, consists of white fibrous tissue, and in the largest veins, particularly in those of the abdominal cavity, there are a few unstriated muscular fibres arranged in a longitudinal direction. In the veins near the heart a few striated muscular fibres are present, derived principally from those of the auricle. These fibres are particularly well developed in the turtle. In certain situations in the cerebral sinuses, etc., the veins consist of little more than the internal coat with a few longitudinal fibres. Generally the veins adhere much more closely to the surrounding tissues than the arteries. Were such not the case, in many instances the vessels would collapse, the walls not being strong enough to resist external pressure. Bernard has called attention to the importance of this physiologically, showing that it is through the intimate adhesion of the wall of the superior vena cava, jugular, subclavian, etc., to the surrounding aponeurotic layers that these vessels are kept open during inspiration.

Many of the larger veins are provided with valves resembling those of the aorta and pulmonary artery (Fig. 205). They are usually found in pairs, and consist of crescentic semilunar doublings or folds of the internal coat or lining membrane of the vein strengthened with some included fibro-elastic tissue. These valves are usually situated opposite

each other and project obliquely into the cavity of the vein or in the direction of the current. The convex portion of each valve is attached to the side of the vein, the concave edge is free and points toward the heart. Behind each valve the vein is dilated into a sort of pouch or sinus (Fig. 205) which prevents the

FIG. 205.



Diagrams showing valves of veins A. Part of a vein laid open and spread out, with two pairs of valves. B. Longitudinal section of a vein, showing the apposition of the edges of the valves in their closed state C. Portion of a distended vein, exhibiting a swelling in the situation of a pair of valves. (QUAIN.)

valves adhering to the sides of the vein as the blood passes between them toward the heart. When, however, the blood passes backward toward the periphery, as we shall see it does under certain circumstances, it enters the sinus and getting behind the valves presses them toward each other and together and so prevents any further reflux.

The valves are so disposed, therefore, that while they offer no obstacle to the flow of the blood toward the heart they effectually prevent to any extent motion in the reverse direction.

The valves are most abundant in the upper and lower extremities; the significance of this we shall see presently. The importance of the valves in the veins, though great physiologically,

must not be exaggerated, since many veins have no valves. Thus in man at least, however it may be in other mammals, there are no valves in the *venæ cavæ*, in the innominate, pulmonary, portal, hepatic, renal, uterine, ovarian, spinal, and iliac veins. Further, there are very few valves in the veins of birds, reptiles, and fishes, and with the exception of that in the aorta, so-called, of the eolis, a small nudibranchiate mollusk, there are none in the veins of the invertebrata. It is evident, therefore, that the valves are not indispensable in the maintenance of the circulation.

The veins possess a considerable amount of elasticity. This is shown by the jet of blood which follows the puncture of a distended vein made in a portion of the vessel between two ligatures. The veins through their unstriped muscular fibres are also contractile, their calibre being slowly and gradually diminished through the application of electrical and other stimuli. The contractility of the veins can be more readily demonstrated in the frog and other batrachians than in mammals. The veins, like the arteries, are supplied and influenced by the vasomotor nerves though not to the same extent. The veins, though much thinner and apparently weaker, will usually resist a greater pressure than the arteries. Thus it was shown in the last century by Wintringham<sup>1</sup> that a greater force was required to rupture the *vena cava* and portal vein, for example, than the aorta. The method by which this was determined is as follows: An iron siphon containing a sufficient quantity of mercury, to which was screwed a glass gauge, and which communi-

<sup>1</sup> An Experimental Inquiry on some parts of the animal structure, pp. 49, 73, 179, 212. London, 1740.



cated freely with a condensing syringe, was adapted to the artery or vein whose strength was to be tested. When the air in the sealed top of the gauge was compressed with a pressure equal to 138 pounds, the aorta in the ram, for example, burst, the vena cava of the same animal, however, resisting until the pressure amounted to 176 pounds, or about 4.8 atmospheres. The strength of the portal vein was even greater than that of the vena cava, a pressure of nearly 5 atmospheres being required to rupture it. Wintringham, however, notices that the arteries of glands are stronger than the corresponding veins. Thus the splenic vein burst under a pressure of about 1 atmosphere, equal to a pressure of about 34 pounds, the artery supporting a pressure of 6 atmospheres, or 150 pounds. These experiments of Wintringham were very numerous and extended, being made upon the vessels of men, pigs, sheep, dogs, etc., and in the main have been confirmed by the later ones of Davy.<sup>1</sup> The significance of the greater strength of the veins, as compared with that of the arteries, usually observed, becomes at once apparent when we reflect upon the different amounts of pressure to which the two sets of vessels are subjected. We have seen that the pressure all throughout the arterial system is about the same, that the force of the heart is practically constant, and that the arterial pressure is being constantly relieved by the flow into the capillaries. On the other hand, the pressure into the veins varies according to the amount of blood delivered to them by the capillaries, regurgitation to any extent is impossible through the presence of the valves, while the heart offers a very restricted outlet. Thus portions of the venous system, from pressure in the veins, absorption of fluid, accumulation through gravity, etc., are subject to very great variations in pressure which the tenacity of their walls usually enables them to resist without injury. The ill effects of over-distention are, nevertheless, seen only too frequently in varicose veins, etc. The capacity of the venous system is much greater than that of the arterial—according to Haller,<sup>2</sup> in the ratio of 2.2 to 1. Usually a vein when distended contains more blood than the adjacent artery; the pulmonary arteries, however, about equal the corresponding veins in capacity. Many arteries, like those of the extremities, are accompanied by more than one vein, and some, like the brachial and spermatic, have more than two; the superficial veins, further, have no corresponding arteries. Nevertheless, any estimate of the capacity of the venous system as compared with that of the arterial can be only approximate, since the quantity of blood flowing through the veins must vary according to the pressure and velocity of the flow, the amount passing through the capillaries, the state of the digestion and respiration, etc. Indeed, the most striking characteristic of the venous system is the variability of the amount of blood it contains.

One of the most important features of the venous system is the numerous anastomoses between the veins, which, it will be remembered, are exceptional in the case of the arteries. There are always numerous such channels by which the blood finds a ready route back to the

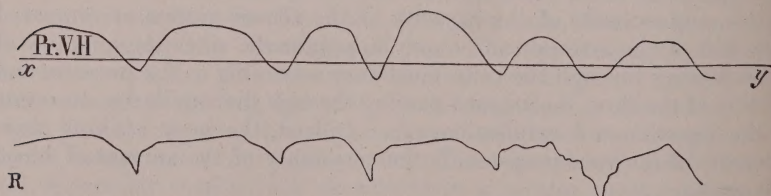
<sup>1</sup> Researches, Physiological and Anatomical, vol. i p. 441.

<sup>2</sup> Elementa Physiologia, tomus I. p. 133.

heart, so that, if the flow be obstructed in one vein, an equally easy way is offered by another. The anastomoses between the veins are very important, enabling these vessels to accommodate themselves to the great variation in the quantity of blood flowing into them to which they are subject. The anastomoses, together with the valves, serve to provide against any obstacle to the freedom of the capillary flow, the importance of which we have already seen. In addition to the anastomotic branches usually described may be mentioned others less well known, such as those connecting the vena cava and portal, like the subperitoneal vessels, the œsophageal and hemorrhoidal, the diaphragmatic connecting the hepatic circulation with the vena cava. The importance of these anastomotic vessels becomes evident when the veins usually returning the blood to the heart are obstructed. Under such circumstances, they become greatly enlarged, as is well known to the pathological anatomist.

When it is remembered that the arterial pressure gradually diminishes as we recede from the heart to the periphery, it might be expected by the time that the blood has passed through the capillaries and reached the veins, that it would exert but little pressure on the latter. This has been experimentally shown to be the case. Thus, according to Volkmann,<sup>1</sup> while the pressure in the carotid artery of the calf amounts to 165 mm. (6.6 inches), and that of the metatarsal to 146 mm. (5.8 inches), the pressure in the metatarsal vein was only 27.5 mm. (1.1 inch). Indeed, at times, the pressure in the vein is actually less than that of the atmosphere. This is well seen in the experiment of Barry,<sup>2</sup> which consists in introducing into the jugular vein of a horse or dog a bent tube, of which the opposite end is immersed in a vase of colored liquor. With each inspiration the liquid rises in the tube, falling again with each expiration. While the pressure is diminished in the jugular and hepatic veins during inspiration, on the other hand, in the remaining abdominal veins it is increased; the latter being compressed by the viscera through the falling of the diaphragm, an obstacle is offered to the flow of the blood, and the pressure rises. The lowering of the thoracic pressure during inspiration is shown graphically by Fig. 206, in which the

FIG. 206.



Trace of blood pressure in hepatic vein. R. Trace of respiration, taken with pneumograph.  
(MAREY)

depression of the upper trace Pr.V. H, representing the blood pressure, coincides with that of the lower trace R, representing the respiratory

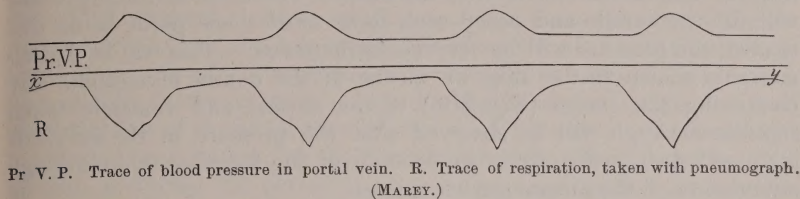
<sup>1</sup> Die Hæmodynamik, S. 173.

<sup>2</sup> Recherches expérimentales sur les causes du mouvement du sang dans les veines. Paris, 1825.



movement. The increase in the pressure in the abdominal vein during inspiration is well shown by Fig. 207, in which the depression in the

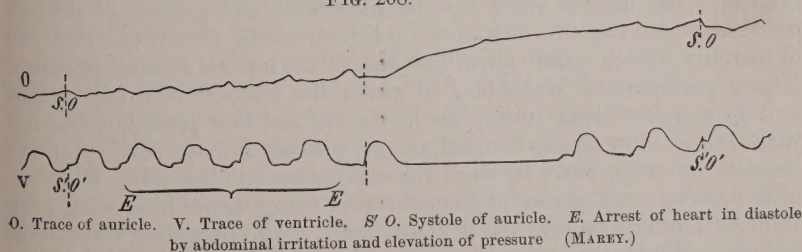
FIG. 207.



lower trace R, due to inspiration, coincides with the elevation of the upper trace Pr.V. P., due to the increase in the blood pressure. On the other hand, during the expiration, the pressure in the abdominal veins is diminished, the viscera no longer compressing these vessels, the diaphragm being elevated. If, however, the expiration be violent, then the contraction of the abdominal walls compressing the viscera and the veins will increase the pressure.

The weight of the blood influences the pressure in the veins. Thus, the blood flows more readily to the heart in the veins of the upper extremity when the limb is elevated than when hanging down. The varicose condition often observed in the veins of the lower extremities illustrates the effect of the venous pressure due to the weight of the blood. While the pressure in the veins is ordinarily very slight, at times it is so much increased as to give rise to a pulsation—the venous pulse. This may be due to an obstruction in the veins, or to an increase in the quantity of blood flowing in these vessels. Thus, if all the venous blood in a part be forced to return to the heart by a single vein, as can be effected by ligating all the adjacent veins, as in the experiment of Poisseuille,<sup>1</sup> the pressure on the vein will be so much increased as to equal that of an artery of like size, the force of the

FIG. 208.



heart being exerted upon the blood of a single vein, and therefore concentrated instead of as ordinarily upon several and, therefore, diffused and dissipated. During the ventricular systole, and, therefore, when the tricuspid valve is closed, the flow of the blood through the auricle into the ventricle is, for the instant, stopped, the pressure in the

<sup>1</sup> Magendie : Leçons sur les phénomènes physique de la vie, tome iii. p. 181. Paris, 1837.

auricle and vena cava is then momentarily increased. If, however, the beating of the heart cease in diastole, as is the case after excitation of the pneumogastric nerve, the blood flows into the ventricle, which, being filled, receives then no more blood from the auricle; the blood continuing to flow will fill the auricle and other vena cava until these parts, being distended, the pressure will be very much increased. This can be experimentally shown in the frog by means of the double myograph. By comparing the traces (Fig. 208) of the auricle and ventricle, taken simultaneously, it will be observed that the pressure in the auricle is increased during the arrest in diastole of the heart's action through stimulation of the pneumogastric nerve.

There is also observed at times in certain veins, the external jugular, for example, a regurgitant venous pulse. This is due to a reflux of blood from the right side of the heart, and is synchronous with the movement of expiration, there being no obstacle at the mouth of the vein to the return of the blood if the expiratory movement be exaggerated. The regurgitant venous pulse can be often noticed, however. It is usually evidence of insufficiency of the tricuspid valve, or some other pathological condition. We have seen that the veins are both larger and more numerous than the arteries, and as the volume of blood which passes in a given moment through any part of the vascular system is the same, it follows that the blood ought to flow more slowly through the veins than the arteries. If the venous system be considered twice as capacious as the arterial, then the blood should flow *quickly* / half as ~~slowly~~ <sup>quickly</sup> through the veins as the arteries. Experiment is in harmony with theoretical considerations, it having been shown by Volkmann<sup>1</sup> that the blood flows in the jugular vein of the dog at the rate of 225 mm. (9 inches) in a second, that of the carotid artery in the same animal being 329 mm. (13 inches). The conditions that influence the rapidity of the flow in the veins, however, vary, so that it is impossible to fix upon any average rate.

There can be no doubt that the flow of the blood in the veins is essentially due to the contractile force of the heart. Thus, according to Sharpey,<sup>2</sup> the hepatic veins can be filled with an injection of defibrinated blood thrown into the aorta under a pressure of 3.6 cm. (3.5 in.) of mercury, which is only about half that of the normal arterial pressure. The experiment of Magendie,<sup>3</sup> in which the femoral vein was ligated and opened, the blood jetting forth, the jet and flow gradually ceasing with compression of the femoral artery, proved the competency of the heart to force the blood through the capillaries into the veins, the force of the artery causing the jet from the vein being, as we have seen, only the reaction from its previous distention, due to the preceding ventricular systole. While the heart is the main cause of the venous flow, as in the case of the capillaries, there are other causes which assist in promoting this movement. Thus, muscular contraction, by compressing the veins, forces the blood in these vessels toward the heart, regurgitation being impossible through the action of the valves. Hence, the

<sup>1</sup> Op. cit., S. 195.

<sup>3</sup> Journal de Physiologie, 1821, t. i. 3.

<sup>2</sup> Todd and Bowman: Phys. Anat., 1856, vol. ii. p. 350.



significance of the fact of valves being so much more numerous in the veins of the muscles than in the cavities of the body, the veins in the latter situation not being subjected to the same kind of compression as those between and within the muscles. It must be mentioned, however, in order that too much stress be not laid upon this connection between muscular action and the presence or absence of valves, that in some cases, as in the portal vein of the horse and in the mesenteric veins of the reindeer, for example, valves do exist. In order that muscular contraction shall assist the flow of the blood through the veins, not only must valves exist to prevent regurgitation, but the contractions of the muscles must be intermittent, as during the period of repose after a contraction the vein has time to fill up again with blood that will be forced forward with the following contraction. This alternate filling up and emptying of the muscular veins is also of advantage from a nutrition point of view, since, as we shall see, the activity of the muscle depends upon the free and rapid circulation of the blood through its substance.<sup>1</sup> The influence of muscular contraction in accelerating the venous flow is well known to every surgeon, the jet from a vein increasing in force with the contraction of the muscles below the opening. The amount of increase of pressure in the veins, due to muscular contraction, can be experimentally determined by placing a vein in communication with a mercurial manometer, and observing the variations in the height of the mercury due to muscular contraction, whether produced naturally or by movements of the animal, or induced by stimuli. In the experiments of Magendie<sup>2</sup> and Bernard<sup>3</sup> the mercury rose 50 mm. (2 in.) above the normal venous pressure after a general muscular contraction. However important muscular action may be in promoting the flow of venous blood, that it is not indispensable, is shown by the fact that the blood flows through the veins in parts that are paralyzed. When we come to study the mechanism of respiration we shall see that the thoracic walls alternately recede and approach synchronously with the rise and fall of the diaphragm in the production of the inspiratory and expiratory movements. It will become apparent, then, that the rarefaction of the air within the thorax during its dilatation, which causes the entrance of the external air into the trachea and the lungs in inspiration, must exercise a similar suction influence upon the blood flowing in the large and extensible veins emptying into the heart. This action of the thoracic walls will have, however, little or no influence upon the blood of the aorta, its walls being too resisting to give to any extent. The suction force thus exerted by the thorax during inspiration upon the venous blood flowing toward the heart extends also, to a certain extent, to the veins situated outside of the thorax. The fact already alluded to, and noticed particularly by Bernard,<sup>4</sup> of the walls of the superior vena cava, jugular, subclavian, etc., adhering to the surrounding tissues by aponeurotic layers, and so, being kept open, evidently favors the flow of blood through these veins toward the heart during inspiration. Were it not for such a disposition the veins would entirely collapse through

<sup>1</sup> Milne Edwards: *Physiologie*, tome iv. p. 310.

<sup>2</sup> *Op. cit.*, tome iii. p. 162.

<sup>3</sup> *Leçons sur la Phys. et Path. du Systeme Veneux*, tome i. p. 285. Paris, 1858.

<sup>4</sup> *Physiologie*, tome iv. p. 9.

atmospheric pressure. The hepatic veins also adhere to such an extent to the tissue of the liver that when divided they remain open, and the inferior vena cava, in which these veins terminate, is further surrounded by fibrous expansions, which fix it to the margin of the diaphragm through which it passes on its way to the heart. The anatomical relations of the parts are such, therefore, as to favor the flow of the venous blood from the liver toward the heart during the contraction and consequent fall of the diaphragm incidental to inspiration. That such a suction force is really exerted upon the venous blood during inspiration by the thorax is seen whenever a violent inspiratory effort is made. At such times the veins at the lower part of the neck are seen to empty themselves completely. The experiment of Barry, already described, illustrates the power of this suction force, the fluid being sucked up into the glass tube introduced into the jugular vein with each inspiration. Barry, however, exaggerated the influence of this suction force. That it does not ordinarily extend much beyond the thorax can be proved by introducing the glass into the anterior end of the jugular vein, when little or no variation will be observed in the level of the liquid with the inspiratory effort.

Death from the entrance of air into the veins is due to the suction force exerted by the thorax during inspiration. The consideration of such cases belongs to pathology, but it may be mentioned here incidentally that the cause of death is due to the blood becoming frothy or spumous when mixed with air, and in that condition ~~will~~ not circulate through the pulmonary capillaries, hence the left side of the heart is found on post-mortem examination empty.

It might naturally be supposed that, as inspiration favors the flow of the venous blood toward the heart, the expiration would oppose it. Were expiration due solely to the contraction of the thoracic walls, such would be, at least to a certain extent, the case, but, as we shall see, the air is expelled during expiration from the lungs to a great extent through the elasticity of the organs themselves, and, as Milne Edwards<sup>1</sup> suggests, this action of the lungs, so far from compressing the veins near the heart, tends to dilate them. A part of the pressure due to contraction of the thoracic walls that would otherwise compress the veins is, therefore, neutralized by the elasticity of the lungs. It can be shown experimentally by the manometer, as the above consideration would lead us to expect, that the effect due to inspiration upon the flow of the venous blood far exceeds that of expiration. The valves, further, while offering no obstacle to the flow of the blood during inspiration, prevent, to any extent, regurgitation during expiration. Thus, if the manometer be placed in the internal jugular vein above the valves, the effect of inspiration is the same as when placed below them, but in the first case the reflux during expiration amounts to nothing. If expiration be violent, however, then the reflux may be considerable, thus the veins of the neck during singing or prolonged speech are seen to swell up, and when any effort is made in which the glottis is closed. The dilatation of the thorax has but little effect

<sup>1</sup> Op. cit., tome iv. p. 419.



upon the blood flowing in the great veins of the abdomen on account of the flaccidity of their walls, but the diaphragm falling during inspiration compresses the viscera, and they in turn pressing upon the vena cava and its branches, force the blood toward the heart, regurgitation toward the extremities being prevented through the closing of the valves. With the rise of the diaphragm the pressure upon the vena cava will be relieved, and the blood will rapidly flow into it again from the extremities. Should the expiration, however, be labored or violent, and the abdominal walls contract, then the pressure exerted upon the viscera would be an obstacle to the flow of the venous blood from the extremities. In order to appreciate the influences of respiration upon the flow of the venous blood, as seen from what has just been said, we must carefully consider the conditions of the inspiration and expiration, as the same cause may, under different circumstances, produce exactly the opposite effect. On the whole, respiration favors the flow of the venous blood from the periphery to the heart, and, as we shall see hereafter, the flow of the arterial blood from the heart to the periphery.

The contractility with which the veins are endowed assists somewhat in the lower animals the flow of the blood. This influence is limited in man, however, to the large veins near the heart, and is even there very slight. Gravity, while favoring the flow of the venous blood from parts above the heart, opposes that from below. While muscular action, respiration, contractility, gravity, etc., no doubt at times favor the flow of the venous blood toward the heart, it must not be forgotten that all these conditions are only supplementary to the force of the heart, this being sufficient to force the blood throughout the entire vascular system. Having described the general manner in which the blood flows through the system, we might now consider the peculiarities presented by the circulation in the lungs, liver, brain, erectile tissues, etc. We will defer, however, our account of the circulation in these organs until we take up their functions. We have seen that the velocity of the blood varies considerably in the different parts of the vascular system, being greatest in the large arteries, least in the capillaries, and intermediate between these extremes in the veins, so far as can be estimated.

It remains for us now to determine if possible, the general rapidity of the circulation; that is, the period necessary to complete the entire circuit, or the time that elapses during which a particle of blood passing out of the left ventricle traverses the arterial, capillary and venous systems, returning by the right side of the heart and lungs to the point from which it started.

The general rapidity of the circulation can be easily and satisfactorily determined experimentally in a living animal in the following manner, as was first done by Hering:<sup>1</sup> A harmless substance, and easily recognized, is injected into the jugular vein, and blood is drawn as quickly as possible, and at intervals, from the corresponding vein of the opposite side of the head, the time being carefully noted when the substance injected can be detected. Suppose, for example, that a solution of ferro-

<sup>1</sup> Zeitschrift für Physiologie Treviranus, 1829, Band iii. p. 85. Archiv f. physiol. Heilkunde, 1853, Band xii. S. 112; 1832, Band v. S. 58.

cyanide of potassium be injected into the jugular vein of a rabbit, the salt can be recognized in the blood of the opposite vein in about seven seconds. In this experiment the blood carrying the salt passes to the right side of the heart, then through the lungs to the left side, from there into the aorta, and traversing the capillaries of the head and face returns back by the jugular vein on the opposite side. If the substance be injected into the femoral vein the period elapsing is slightly longer, the vessels through which the blood flows being somewhat longer. This is more evident, however, in a large animal like a horse, than in a small one like a rabbit. Ferrocyanide of potassium is not only used in this experiment on account of it being harmless, but from the readiness with which its presence can be determined in the blood. Vierordt<sup>1</sup> improved somewhat Hering's method by collecting the blood as it flowed at small intervals in little vessels that were fixed to a disk which revolved at a fixed rate, the time being determined a little more accurately. The results of the experiments of both these observers, however, agree essentially. According to Hering, the rapidity of the circulation in an animal is inversely as its size, and directly as the rapidity of the action of its heart. Thus, while in the rabbit we have seen that the circulation from jugular to jugular is accomplished in 6.9 seconds, in the goat, dog, and horse, 12.8, 15.2, and 27.3 seconds are required respectively.

TABLE LV.—RAPIDITY OF CIRCULATION.

|                                                       |           |
|-------------------------------------------------------|-----------|
| Ventricle contracts in a minute . . . . .             | 72 times. |
| Amount of blood expelled at each contraction . . . .  | 4 oz.     |
| Amount of blood passing through ventricle in a minute | 288 oz.   |
| 16 lbs. of blood in the body.                         |           |
| 16 oz. to lb.                                         |           |
| 256 oz.                                               |           |
| 60 : 288 oz. of blood :: $x$ sec. : 256 oz. of blood. |           |
| 288 $x$ 256 $\times$ 60                               | 15360     |
| $x = \frac{15360}{288} = 53.3$ seconds.               |           |

The general rapidity of the circulation in man can be deduced, at least approximately, from these experiments, about thirty-two seconds probably being required for the blood to pass from jugular to jugular. On the supposition that the heart beats seventy-two times in a minute, and that at each ventricular systole four ounces of blood are forced into the aorta, it is evident that 288 ounces of blood ( $72 \times 4$  equals 288) pass through the heart in one minute; but we have seen that there are probably, on an average, only 256 ounces (16 pounds) of blood in the body. It follows, therefore, that less time than one minute, or about fifty-three seconds, would be required for the whole mass of the blood to pass through the heart. Table LV. shows, synoptically, the calculation by which this estimate is made. The only objection to this manner of determining the time required for the whole mass of the blood to pass through the heart is the uncertainty as regards the exact

<sup>1</sup> Die Erscheinungen und Gesetze der Stromgeschwindigkeiten des Blutes, etc., S. 65.



amount of blood in the body, and of the quantity expelled with each ventricular systole. From the nature of the case these data must be variable; the estimate will be true, however, within limits.

In confirmation of what has just been said in reference to the rapidity of the general circulation, etc., it may be mentioned that the time elapsing between the introduction of a poison into the blood and its characteristic effects is about the same as that observed in the experiment of Hering. The influence of the frequency of the heart's action upon the rapidity of the general circulation must not be lost sight of, and this was taken into consideration also by Hering. It was shown by this observer, contrary to what might have been expected, that an increase in the number of the beats of the heart, whether induced physiologically or pathologically, diminished the rapidity of the circulation instead of increasing it, the force of the heart being diminished as the number of its beats was increased.

## CHAPTER XXV.

### HISTORY OF THE DISCOVERY OF THE CIRCULATION OF THE BLOOD.

IN the minds of every one the circulation of the blood is invariably and justly associated with the name of Harvey. The discovery of the circulation, however, like all other great discoveries, was not made by Harvey alone. Indeed, the discovery of the circulation of the blood, in the widest acceptance of the term, cannot be attributed to any one person, age, or country. With the name of Harvey must be associated those of Erasistratus, Galen, Servetus, Cæsalpinus, Malpighi, Aselli, Pecquet, Rudbeck, and Bartholinus. The history of the circulation extends, therefore, over a period of 2000 years, from the epoch of the Egyptian Ptolemies to the latter part of the seventeenth century, and even, in some respects, to the present day. The general structure of the heart, its cavities, the play of its valves, the passage of the blood from its right side to the lungs and back to its left side, thence through the arteries to all parts of the body; the valves in the veins; the flow of the venous blood toward the heart, had been demonstrated, in an isolated way, by this or that person, before Harvey's time; while it was not until after the appearance of his great work that the discovery of the capillaries made intelligible the manner in which the blood passed from the arteries to the veins; and the demonstration of the lymphatics completed our otherwise imperfect knowledge of the circulation. If, however, the great generalizations as regards the circulation, just referred to, were made either before or after the time of Harvey, naturally, it might be asked, What was there left for Harvey to discover? In what does the merit of his great work consist? In that he was the first to describe accurately the motions of the heart, and both the pulmonary and systemic circulations correctly. Without doubt, Harvey was the first who described correctly the entire circulation of the blood, understanding by the word circulation the flowing of the blood from the heart to the lungs, back to the heart, thence through the arteries to the periphery, and from the periphery, through the veins, back to the heart. That is, the flowing of the blood in a circle. It must be remembered, however, that Harvey saw this circulation only in his mind's eye, as the capillaries or connecting links between the arterial and venous systems were not discovered by Malpighi until after Harvey's death. The history of the discovery of the circulation of the blood has often been told; but the subject is one of such interest, extending as it does over a very long period, illustrating so forcibly how slowly truth is attained, that fact after fact must be first established before any generalization can be arrived at; how the isolated, unconnected labors



of generations finally culminate, in the hands of a genius, in a grand discovery; that I trust it will not be considered superfluous if I rapidly tell the story of the discovery of the circulation of the blood once more. Although no mention is made of bleeding in the *Iliad*, that encyclopædia of the knowledge possessed by the Greeks in Homer's day, yet there is no reason to doubt that Podalirius, who attended, as surgeon, the hosts of Agamemnon, made use of this practice; as we learn from later sources<sup>1</sup> that, by bleeding the daughter of the King of Caria, he effected a cure, the reward of which was her hand in marriage, and, as dowry, the Chersonesus. While the Greeks and the ancients generally were aware that the blood of man and animals coursed in a vast system of tubes, their knowledge of the circulation of the blood extended but a little beyond this. Indeed, their views on this subject were of the most imperfect or erroneous character. That the blood flowed in certain veins; that there were additional vessels erroneously called arteries, because they were supposed to contain air; that the heart was a hollow, muscular organ, constituted about all their knowledge of the circulation.<sup>2</sup> This is not to be wondered at, however, since the superstitious respect paid to their dead by the Greeks made dissection an impossibility, the little anatomical knowledge existing in the days of Hippocrates having been derived from the rapid inspection of the viscera of animals sacrificed upon the altar on the occasion of some religious ceremony. Even Aristotle,<sup>3</sup> whose anatomical knowledge far exceeded that of Hippocrates, advanced but little our knowledge of the vascular system. Aristotle taught that the veins communicate with the heart; that vessels pass from the heart to the lungs, and that the heart and veins are filled with blood. Such was the limited knowledge of the circulation of the blood as known to the most celebrated of the Greeks. A great advance, however, was soon to be made, not only in anatomy, but in all branches of science. The wonderful campaigns and victories of Alexander, Aristotle's patron, resulting in the conquering of Egypt and the establishing of the Macedonian dynasty of kings, and the building of Alexandria not only revolutionized the political and social world, but influenced all branches of knowledge in a way and to an extent that modern Europe is only now beginning to appreciate. Under the magnificent patronage of the Ptolemies, the Macedonian kings of Egypt, there arose at Alexandria that famous school, the Museum, a centre of learning for the organization and development of all kinds of knowledge, the like of which has never been seen since. There were associated under the hospitable roof of the Egyptian kings some of the most learned and wonderful men the world has ever seen. The astronomers, Hipparchus and Ptolemy; geometers like Euclid and Archimedes; the engineers and geographers, Apollonius, Erastosthenes; historians like Manetho; the theologian, Cyril; learned women like Hypatia; the celebrated anatomists and physicians, Herophilus and Erasistratus. For the practical study of astronomy there were placed

<sup>1</sup> Stephani Byzantini: De Urbibus. p. 686. Lugd. Bat., 1694.

<sup>2</sup> Hippocratis' Opera Omnia, p. 275. Lugd. Bat., 1665. Œuvres complètes d'Hippocrate, par E. Littré. Tomes viii. Paris, 1839-1853. Introduction, tome i. p. 241.

<sup>3</sup> Ἀριστοτέλους Περὶ Ζῴων Ἱστορία, Lib. iii. Cap. 2, 3, 4. Lipsæ, 1869.

beneath the Porch equinoctial and solstitial armils, quadrants, dioptras, astrolabes and meridian lines; a botanical garden offered opportunity to those who wished to study plants; a zoölogical menagerie offered facilities to those interested in the dissection of animals. The library, containing nearly a million volumes, was open daily to those desirous of making themselves acquainted with the knowledge of the day or of that of antiquity. Vast collections of all kinds of natural objects had been brought there, from every part of the known world, by the Macedonian conquerors, for the use and benefit of the student. At the Museum, in Alexandria, the student found everything that would assist, develop, and refine the intellect—the calm, the leisure, the means of living and of study. The usages of that wonderful country, Egypt, where death perpetuates itself in a thousand embalmed forms, had, from time immemorial, familiarized the vulgar and uneducated with autopsies and dissections. The study of anatomy by the only means possible, the dissection of the dead body, was no longer regarded with superstitious horror and considered as sacrilege. Pliny tells us that those intelligent and magnificent princes, the Greek kings of Egypt, not only lavished their treasure in the interests of science, but personally attended the dissections that were daily conducted at the Museum. The Medical School of Alexandria gave to the world those famous anatomists, Herophilus and Erasistratus. With them began the study of the structure and use of the heart and its great bloodvessels, by means of actual dissection.

The name of Herophilus ought to be familiar to all students of anatomy, as many parts of the human body, such as the choroid plexus, the torcular Herophili, the calamus scriptorius, the duodenum, etc., were first described by him. The most important contribution that he made to our knowledge of the vascular system was the demonstration of the isochronism of the pulsations of the arteries and of the beating of the heart, and of the latter being the cause of the former, a phenomenon that had already been imperfectly referred to by Hippocrates and Aristotle. Herophilus noticed also the difference in the thickness of the walls of the arteries and of the veins, and described the vessels connecting the heart and the lungs, distinguishing the pulmonary artery from the pulmonary vein, designating the former as the arterial vein and the latter as the venous artery.

To Erasistratus, one of the most distinguished of the anatomists of the Alexandrian school, and one of the most celebrated physicians of antiquity, science is indebted for the discovery of the valves of the heart, and their function in the circulation. It was stated in a previous chapter that there is reason to believe that Erasistratus had seen the lacteals a dependence, so to speak, of the vascular system, even though he had misunderstood their use, and we shall see hereafter that he appears also to have distinguished the sensory from the motor nerves. While there is no doubt that the anatomists and physiologists of antiquity distinguished two kinds of vessels, arteries and veins, their very name, artery, from the Greek *αἷρ*, air, and *τηρεω*, I guard or keep, conclusively proves how absolutely ignorant they were of the two functions of these vessels. Hippocrates, Aristotle, and more especially Erasistratus,



believed that the arteries, as their name implies, carried air. This error was due, no doubt, to the fact that when a dead body is opened the arteries are usually found empty; and to the theory that the air in these vessels came, originally, from the trachea, hence the name of tracheal artery, by which it is designated by the French, even at the present day. Erasistratus<sup>1</sup> supposed the air passed from the trachea into the pulmonary veins (his venous artery), from there to the left side of the heart, and thence, by the arteries, to all parts of the body. Substitute for the air oxygen, and for his venous artery pulmonary capillaries, and the much-abused theory of Erasistratus becomes the modern one of respiration. Although during the four centuries that followed the brilliant epoch of the Alexandrian school just described, dissection had gradually fallen into disuse, nevertheless the most famous anatomist of antiquity, Galen, learned his anatomy in Egypt, where he devoted many years to anatomical studies. His dissections, however, appear to have been limited to animals. By ligating in a living animal, an artery in two places, and opening the vessel between the ligatures, Galen<sup>2</sup> demonstrated that the vessel contained blood. Thus, by an experiment upon a living animal, a vivisection, the first great source of error, that of supposing that the arteries contained air, was removed, the true nature of an artery demonstrated, and the modern theory of the circulation of the blood made possible. Too much importance cannot be attached to this cardinal experiment of Galen. It is evident that as long as it was believed that the veins alone carried blood, and that the arteries only contained air, the discovery of the circulation was an impossibility.

For 1300 years, in anatomical and physiological matters, the authority of Galen was supreme. With the truths discovered by this most deservedly famous physician, were perpetuated errors, among which was Galen's theory that the air inspired did not enter into the body to any extent, as Erasistratus supposed, but was at once rejected after having performed its office, which was that of cooling the body, and that the cavity of the right ventricle of the heart communicated with that of the left ventricle by means of holes in the septum.<sup>3</sup> It is true that no one had seen these holes in the septum, separating the ventricle; even Galen himself did not claim that he actually saw them; but the theory in Galen's time, and many a day afterward, was, that the spirituous blood of the left ventricle must be mixed with the coarser blood of the right ventricle, that the latter should fulfil its function in nutrition. Now the only way that theory could account for this mixing of the two kinds of blood was on the supposition that the septum of the ventricle was perforated with holes, through which part of the blood passed from one ventricle to the other, the rest of the blood passing through the pulmonary artery to the lungs.

Men saw, or believed they saw, what theory demanded they ought to see. As has been too often the case, as the history of science teaches us, the theory did not follow from the facts, but the facts were made to suit the theory. Further, when it is remembered that for sixteen cen-

<sup>1</sup> Galenus edit. cit.

<sup>2</sup> Galenus, edit cit. an sanguis in arteriis natura contineatur, Cap. 6.

<sup>3</sup> Galenus, edit. cit. De usu partium, Lib. vi. Cap. 17.

turies, during the period extending from the epoch of the Alexandrian Museum to that of the School of Salerno, in 1224,<sup>1</sup> or more probably to that of Mundini, in 1306,<sup>2</sup> the human body had never been dissected, it is not to be wondered at that the grossest ignorance of anatomy should have universally prevailed. The horror with which dissection was regarded, and the limited number of subjects obtainable for study, will be appreciated from the fact that Mundini, who was Professor of Anatomy at Bologna during the latter part of the thirteenth and beginning of the fourteenth century, had dissected in eleven years only three human bodies. Berenger de Carpi, who also occupied the Chair of Anatomy in Bologna a century later, had better opportunities of study than Mundini, whose works he commentated, he having dissected a hundred bodies; and yet the authority of Galen had such weight with De Carpi, that he states that there are certainly holes in the septum separating the ventricles. He adds, however, as if he had an uneasy suspicion as to the truth of the statement, that these holes are seen in man with great difficulty.<sup>3</sup>

A short time, however, after the publication of De Carpi's work, viz., in 1553, there appeared the *Christianismi Restitutio* of the Spaniard, Michael Servetus, whose career reads rather like that of the hero in some romance than of a real historical personage. Educated for the priesthood at Saragossa, relinquishing such studies for that of the law, at Toulouse; accompanying, as secretary, Quintana, Confessor to Charles V., upon the occasion of the imperial coronation at Bologna; and going afterward to the Diet of Augsburg; giving up the prospect of a diplomatic career for that of a theologian; leaving Switzerland and changing his name to Villanovus, to avoid persecution; supporting himself as a proof-reader and editor of learned books while a student of medicine in Paris; receiving his degree of doctor in medicine; writing works on medical subjects, and practising medicine with great success for a number of years; returning to the study of theology again, his career of usefulness is suddenly cut short by death at the stake; Servetus, as is well known, being burned alive, in 1553, at Geneva, for heresy, as the author of the *Christianismi Restitutio*. This work, as its name implies, is a theological treatise, but it is also of the greatest interest to the physiologist, as in discussing the nature of the vital spirit, and the manner in which it is elaborated, Servetus describes the flow of the blood from the right ventricle of the heart, by the pulmonary artery, through the lungs, and by the pulmonary veins to the left ventricle; distinctly stating that the blood does not pass from the right ventricle to the left through the septum of the heart, as is commonly believed, but by a long passage through the lungs, from the right ventricle, and that it is in the lungs that the blood is agitated, prepared, and changes its color, thence passing to the left ventricle by the pulmonary veins. Servetus was not only the first to describe, therefore, the flow of the blood from the right side of the

<sup>1</sup> Hæser: Geschichte der Medicin, S. 733-738. Jena, 1875. Corradi: Rendiconde del R. Institut. Lombardo, Ser. ii. vol. vi.

<sup>2</sup> Hyrtl: Das Arabische und Hebraische in der Anatomie, p. 11. Wien, 1879.

<sup>3</sup> Berenger de Carpi. Commentarii cum amplissimis additionibus super anatomia Mundini. Pp. 341. Bologna, 1521.



heart, through the lungs, to the left, and the imperviousness of the septum of the heart, but was also the first to point out the place where the venous was changed into arterial blood, the significance of which discovery was neither understood nor appreciated for more than a century afterward. Further, Servetus adds that the left ventricle is not sufficiently capacious for so copious a mixture, nor will it suffice for the elaboration of the color; and that the septum is neither fit for the communication nor the elaboration of the blood, even if any may exude through it. Servetus evidently does not consider that any blood passes through the septum of the heart, for he most distinctly says that none does so, and in confirmation of his view adds that even if any blood does pass through the septum, the left ventricle is not adapted to its elaboration. That Servetus did not hold the view of Galen, of part of the blood passing through the pulmonary artery and part through the septum, is evident from what Servetus says, that if any one compares his views with Galen's (and no one understood Galen better than Servetus), he will perceive clearly the truth not observed by Galen himself. The celebrated passage upon the pulmonary circulation, in the *Restitutio*, is found in Liber Quintus, De Trinitate Divina, In quo agitur de Spiritu Sancto, p. 170. It is as follows:

“For which purpose the substantial generation of the vital spirit itself is first to be understood, which is composed of and nourished by the inspired air and most subtile blood. The vital spirit has its origin in the left ventricle of the heart, the lungs aiding, to the highest degree, in its generation. The spirit is subtile, elaborated by the force of heat, of a yellowish color, with the power of fire, to the end that it may be, as it were, a bright vapor from the purer blood, containing in itself the substance of water, air, and of fire. It is generated, in fact, in the lungs, with the mixture of inspired air with the elaborated, subtile blood which the right ventricle of the heart communicates to the left. Yet this communication is made, not by the middle wall of the heart, as is commonly believed, but the subtile blood is driven, by a great plan or device, from the right ventricle of the heart, by the long passage through the lungs; is prepared in the lungs; the yellow color is made, and it is poured out from the arterial vein (*vena arteriosa*), or pulmonary artery into the venous artery (*arteria venosa* or pulmonary vein); there is mixed in the venous artery itself with the inspired air; is purged by expiration of its fuliginous matter; and so, at length, the whole mixture is attracted by the diastole from the left ventricle of the heart, a fit stuff out of which to make vital spirit. The various connection and communication of the arterial vein with the venous artery teaches that the communication and preparation is made by the lungs in this manner. The remarkable size of the pulmonary artery confirms this, which would be neither made in such a way nor so large, nor would there be emitted so great a mass of blood from the heart itself into the lungs, if for the nourishment of these alone, nor would the heart serve the lungs in this manner, since, especially before, in embryo, the lungs themselves are accustomed to be nourished from elsewhere, on account of those little membranes, or valves of the heart, not yet being open until the hour of birth, as Galen teaches. Therefore the blood is poured forth, and so copiously,

from the heart into the lungs at the hour of birth, for another use. The air also is sent from the lungs to the heart by the venous artery, not pure, but mixed with blood; therefore the mixture is made in the lungs. That yellow color is given to the blood by the lungs, not by the heart. The space in the left ventricle is not capable of holding so great and so capacious a mixture, nor is sufficient for that elaboration of color. Finally, that middle wall, as it is wanting in vessels and power, is not fit for that communication and elaboration, even if some might sweat through. By the same plan by which the transfusion is made from the vena porta to the vena cava, with reference to the blood, so the transfusion from the arterial vein to the venous artery is made in the lungs, with reference to the spirit. If any one compares this with that which Galen writes, Lib. vi. et vii., on the use of the parts, he easily perceives the truth, not observed by Galen himself. And so the vital spirit from the left ventricle of the heart is thence poured out into the arteries of the whole body."

The *Christianismi Restitutio* is a very rare work. At the present moment there are, indeed, only three original copies known to exist—one in the National Library at Paris, one in the Imperial Library at Vienna, and one in the Library of the University of Edinburgh. The copy in Paris probably belonged to Colladon, Calvin's lawyer, since his name is in it, and was in the possession of the celebrated Dr. Mead, of London, in the early part of the eighteenth century, from whose hands it passed successively through those of de Boze, de Cotte, Gaignat, la Vaillere, finally becoming the property of the National Library. There is not the slightest reason to suppose that the Paris copy of the *Restitutio* was ever in the flames that enveloped its author, as is picturesquely described by Flourens,<sup>1</sup> the blackness on the pages being due, not to fire, but possibly to dampness.<sup>2</sup>

In the year 1555, two years after the printing of the *Christianismi Restitutio*, there appeared the second edition of the magnificent *Anatomy* of Vesalius, which differed in many important respects from the first edition of 1543; among others, as regards the description of the heart. In the 1555 edition, Vesalius begins by saying that, influenced by the views of Galen, he considered that the blood passed from the right to the left ventricle of the heart, through the septum, by means of the pores. He immediately adds, however, that the septum of the heart is as thick, dense, and compact as the rest of the heart, and not the smallest quantity of the blood passes through the septum. There can be no doubt that Vesalius held that the septum of the heart was imperforate, in this (the 1555) edition; but the passage in which he maintains this view is not to be found in the 1543 edition; and yet, in all of the accounts of the history of the circulation with which I am familiar, that of Tollin<sup>3</sup> excepted, the views of Vesalius in reference to the imperviousness of the septum of the heart (printed in 1555),<sup>4</sup> are said to have preceded those of Servetus (printed in 1553). The only

<sup>1</sup> *Histoire de la découverte de la Circulation du Sang*, p. 155. Paris, 1857.

<sup>2</sup> Henri Tollin: *Die Entdeckung des Blutkreislaufs, durch Michael Servet*, p. 69. Jena, 1876.

<sup>3</sup> *Die Entdeckung des Blutkreislaufs*, etc., p. 26. Jena, 1876.

<sup>4</sup> *Andree Vesalii: De Humani corporis fabrica Libri septem*. Basilee, 1555



way in which I can account for this error is by supposing that the historians of the circulation, in quoting Vesalius, have made use of the 1555 or 1725 editions, and not that of 1543. Certainly Servetus did not learn his anatomy from Vesalius, since they were, at the same time, prosectors for Guntherus, Professor of Anatomy in the Medical School of Paris; and as to Servetus's knowledge of practical anatomy there can be no doubt, Guntherus testifying to that.<sup>1</sup> On the other hand, Vesalius was probably entirely ignorant of what his former associate in the dissecting-room had published about the heart.

While, to my mind, there is no doubt that the pulmonary circulation was correctly described by Servetus, beyond statements like that of the blood being transmitted by the left ventricle to the aorta, and thence through the arteries to the whole system, and of the blood flowing from the vena porta through the liver to the hepatic vein, etc., I can find nothing in his work to warrant the view that Servetus had any idea of the so-called systemic or general circulation. Further, it is not to be supposed that Servetus understood the exact manner in which the blood passed from the pulmonary arteries to the veins, since the capillaries were not discovered by Malpighi for more than a century afterward.

Six years after the death of Servetus—that is, in 1559—the pulmonary circulation was re-described by Colombo, who taught anatomy at Padua, Pisa, and Rome. In a work on anatomical subjects, Colombo, in speaking of the heart, observes that between the ventricles a septum is present, through which almost every one believes that the blood passes from the right ventricle of the heart to the left, but that really the blood goes through the pulmonary artery to the lungs, and is then carried, with the air, by the pulmonary vein, to the left ventricle of the heart, and that no one had previously observed or described this.<sup>2</sup> Colombo, however, is evidently wrong when he says no one had previously observed or described this. It is possible that Colombo was ignorant of what Servetus had written in his *Christianismi Restitutio*, but it certainly appears to me very extraordinary, if such was the case, for Colombo was the pupil of Vesalius, and taught, as prosector and professor, for years, in Padua, the very city where Servetus had sent one of the manuscript copies of his work, and where his views were well known. Whether Colombo was acquainted with the writings or the views of Servetus may be a question, but there can be no doubt that he understood and described the pulmonary circulation. This able anatomist, however, held entirely erroneous views as regards the general or systemic circulation, for, in speaking of the liver and veins, in the same work that we have just referred to, he distinctly states that the liver is the head, the fountain, the origin of all the veins.<sup>3</sup> It is evident that one who held, with Galen, that the veins originated in the liver, the venous blood being transmitted thence to the periphery, could have no idea of the general circulation.

In 1571, eighteen years after the death of Servetus, there appeared

<sup>1</sup> Haller *Bibliotheca Anatomica*, tomus i. Tiguri, 1774.

<sup>2</sup> Realdi Columbi Cremonensis in alino Gymnasio Romano Anatomici celeberrimi de re Anatomica, Libri xv.; Lib. vii. de corde et Arteriis, p. 177. Venetiis, 1559.

<sup>3</sup> De jecore et venis, p. 164, op. cit.

the *Quæstionum Peripateticarum* of Cæsalpinus,<sup>1</sup> one of the most distinguished of the many celebrated men that Italy produced in the sixteenth century. Cæsalpinus taught medicine at Pisa, and was afterward physician to Pope Clement VIII. at Rome, and was as distinguished a botanist as a physician, being the first to classify plants according to a natural method, and may be justly regarded as the father of vegetable anatomy. Cæsalpinus described the pulmonary circulation, observing that the circulation of the blood from the right ventricle of the heart, by the lungs, to the left ventricle of the same, agrees best with what appears from dissection. One can hardly believe that such a learned man as Cæsalpinus was unaware of the views of Servetus or Colombo; certainly, at least, of the existence of the *De re Anatomica*, published so recently as 1559, and by an anatomist who taught in the neighboring city of Padua; and yet he mentions neither.

It is strange, however, that if Cæsalpinus's views upon the pulmonary circulation were derived from either the works of Servetus or Colombo, he should have held, with Galen, as he undoubtedly did, that the septum of the heart was pervious, part of the blood passing directly from the right to the left ventricle, which both Servetus and Colombo showed was not the case. Had Cæsalpinus published nothing more than his *Quæstionum Peripateticarum*, there would have been no necessity for my referring to that philosopher in connection with the history of the discovery of the circulation of the blood. Twelve years afterward (1583), however, the *De Plantis*,<sup>2</sup> by the same author, appeared, and this work has the greatest interest for us, as for the first time the general or systemic circulation, with the exception of the capillaries, is described, though it must be admitted that the description is very brief, and supported by little or no experimental evidence. In this work Cæsalpinus distinctly says that the food is carried by the veins to the heart, and thence, by means of the arteries, is distributed to all parts of the body. Cæsalpinus not only understood the way in which nutriment is distributed throughout the economy, but, with the exception of the capillaries, the manner in which the blood flows through the system. For in his *Quæstionum Medicarum* (p. 234) Cæsalpinus calls attention to the fact that when the veins in the neck are compressed the swelling of the veins is between the brain and ligature, not between the ligature and the heart, and draws the conclusion that just the opposite ought to happen—that is, the swelling ought to be between the ligature and the heart, if the motion of the blood in the veins is from the heart and other viscera to the periphery of the system, as was the general opinion at that time. Cæsalpinus continues, in the same page, by saying that there is a perpetual motion of the blood from the vena cava, through the heart and lungs, to the aorta, and that the arteries communicate with the veins by what are called anastomoses; that the blood flows to the upper parts and returns, Euripus-like, to the lower ones, is perfectly evident, both when one is asleep and awake, and that this motion is not obscure in any part of the body when you experiment by binding veins or

<sup>1</sup> Andrea Cæsalpini Aretini Quæstionum Peripateticarum, Lib. v. Quæstio iv. p. 125. Venetiis, 1593.

<sup>2</sup> De Plantis Libri. xvi. Lib. i, Cap. ii. p. 3. Florentiæ, 1583.



occluding them in any other manner. The above distinct, concise statements appear to me to prove that Cæsalpinus understood the systemic circulation, as far as was possible for one who had never seen the capillaries; as regards the pulmonary circulation he undoubtedly also states that the blood passed from the right side of the heart to the left, by the lungs; but, as we have seen that, in the *Quæstionum Peripateticarum*, he says that part of the blood passes through the septum, and as he does not contradict this statement, but refers to this work as containing his views, he could only have understood the pulmonary circulation imperfectly. By most of those who have written on the discovery of the circulation, a very different interpretation, however, is offered of the views of Cæsalpinus from that just given. By such, it is stated that Cæsalpinus held that there was a to-and-fro motion of the blood in the veins, Euripus-like; that the arteries communicated with the veins only during sleep; that the blood only irrigated the tissues, but did not circulate through them, etc. If these are the views of Cæsalpinus, then he certainly did not understand the circulation in any part of its course.

In order that the reader may judge for himself, as to what the views of Cæsalpinus really were, I will give the passage from his *Quæstionum Medicarum*<sup>1</sup>—to which I have referred, and will say but a word further concerning it.

But that appears worthy of observation, for the reason that the veins swell up from a bandage on the other side of the seat of application, not this (toward heart), which those know from experience who bleed; for they apply the bandage this side of the position of section, not on the other side, because the veins swell up on the other side of the bandage, not this side. But the opposite way ought to happen if the motion of the blood and spirit is made from the viscera into the whole body, for the canal being intercepted, progression is not given, therefore, the swelling of the veins ought to be made on this side of the bandage. Or, indeed, our doubt is solved from that which Aristotle writes of sleep, Chap. 3, where he says, "Necessarily what is evaporated, impelled continually elsewhere, is then turned back and changed, like the Euripus; for the heat of any animal is intended by nature to be carried to the higher parts, much, at the same time, on the other hand, is turned back and carried downward." So, Aristotle. For the explanation of this passage, we must know this. That the cavities of the heart are so prepared by nature that there is an opening made from the vena cava into the right ventricle of the heart, when an exit into the lungs is opened. Further, from the lungs there is another opening into the left ventricle of the heart, from which, finally, an exit is open into the arterial aorta, the valves of which are placed at the mouths of the vessels, in order to impede retrogression. For thus there is a perpetual motion from the vena cava, through the heart and lungs, to the arterial aorta, as we have explained in the peripatetic questions. But since, when we are awake, the motion of the native heat is outward, that is, toward the sensorium, but in sleep inward,

<sup>1</sup> Andreæ Cæsalpini Aretini, *Quæstionum Medicarum*, Libri ii. pp. 233, 234. Venetiis, 1593.

that is, toward the heart, we must be led to think that while we are awake much spirit and blood are carried to the arteries, for thence is the way to the nerves. But in sleep the same heat reverts, by the veins, to the heart, not by the arteries, for the natural entrance to the heart is given by the vena cava, not by the artery. The evidence of this is the pulses, which, while we are awake, are made great, vehement, rapid, swift, with each vibration, but in sleep small, languid, slow, infrequent (3 de can. pul. 9 and 10). For in sleep the native heat tends less toward the arteries, it bursts forth into the same most vehemently when they are awake. But the veins have a contrary habit, for in sleep they become more swollen, and when we are awake more empty, as is evident by observing those which are in the hand. For the native heat in, sleep, passes from the arteries to the veins by their common mouths, which they call anastomoses, and thence to the heart. But the pouring out of the blood to the higher parts and its retrocession to the inferior ones, like that of the Euripus, is manifest in sleep and when we are awake, for this kind of motion is not obscure in whatever part of the body the bandage is applied, or by whatever other means the veins are closed up. For when the permeation is allowed, the rivulets swell up in parts by which they are accustomed to flow. The blood recurs powerfully at that time to its source, lest, having been cut off, it be extinguished.

It will be observed that in this passage the word Euripus occurs twice. In the first instance, however, it is Aristotle that uses it, expressing by it in a metaphorical way, his view as to the ebb and flow of the heat of an animal; Euripus being a narrow sea between Bœotia and Eubœa, which, according to the ancients, ebbed and flowed several times a day. Hence, we find several writers using the word Euripus to express an oscillation of any kind. As we are not concerned at present with what Aristotle or Cæsalpinus thought of animal heat, it is not necessary to dwell further upon this part of the passage, simply mentioning that Cæsalpinus says nothing as regards the heat as evidenced by the pulse, etc., which is inconsistent with what is known at the present day, the heat going to the heart by the veins, not by the arteries. In the second instance where the word Euripus occurs, Cæsalpinus uses it metaphorically, in the sense of an oscillation; but in this case, as applied to the blood. It is distinctly stated that the blood is poured out toward the superior parts, and retrogrades to the inferior ones, both asleep and awake. The ebb and flow is from the heart to the head and back again, by the arteries to the head, by the veins to the heart, there being a perpetual motion from the vena cava to the heart, through the lungs back to the heart, and so to the arteries; thence the way to the nerves, the nerves being nourished by arterial blood, like all the other structures. Not a word is said of there being an ebb and flow, a Euripus-like motion, in the veins; on the contrary, it is distinctly said that blood flows in the veins toward the heart, as can be proved by binding up a vein anywhere. It will be observed that Cæsalpinus says that the natural heat passes, only during sleep, from the arteries to the veins, by anastomoses. This statement, however, is a totally different one from



saying that the arteries anastomose only with the veins during sleep. If there are anastomoses during sleep, there are anastomoses during the wakeful condition. More heat may be generated and transmitted through the economy at one time than another, but the absence of all heat would not affect the existence of the anastomoses. Cæsalpinus, so far from saying that the blood passes from the arteries to the veins only during sleep, says that the motion of the blood is perpetual, during both the sleeping and waking conditions. That Cæsalpinus understood that the blood circulated, and did not simply irrigate the system, seems to be proved by the fact of his saying that the blood circulates in one work, in another that the blood is carried by the veins to the heart, and from the heart by the arteries, and that the arteries anastomose with the veins, and that the motion is perpetual from the vena cava to the heart and lungs to the aorta. It is not to be implied, however, that he understood the exact manner in which the blood passed from the arteries to the veins because he uses the word anastomoses. Galen and Servetus used the same word in this connection, as also afterward Harvey, although there is no reason to suppose that these writers ever meant, by the word anastomosis the capillaries, and yet, without a knowledge of these vessels, the systemic, no more than the pulmonary circulation, could be thoroughly understood.

It will be seen, from this brief *résumé* of the views of Servetus, Colombo, and Cæsalpinus, that while the pulmonary circulation (with the exception of the capillaries) was understood by Servetus and Colombo, they had but little or no idea of the general or systemic circulation; on the other hand, while the general circulation (with the exception of the capillaries) was correctly described by Cæsalpinus, he understood the pulmonary circulation only imperfectly. It cannot be said, therefore, that any one, up to the end of the sixteenth century, understood the entire circulation of the blood, using the word circulation in the sense that we do at the present day. Isolated portions of the circulation only had been described. It remained now for some one to show the connection between the facts already established, to add important new ones, to offer a view based upon observation and experiment that would explain all the facts. In a word, to demonstrate that the blood actually circulates.

It is claimed by some writers that this honor should be accorded to Carlo Ruini, of Bologna, it having been asserted that Ruini discovered both the pulmonary and systemic circulations. Even if Ruini had described both the circulations correctly, that would not have entitled him to be called their discoverer, since the pulmonary circulation had been previously described by Servetus and Colombo, and the systemic circulation by Cæsalpinus. Ruini does not appear to me, however, to have thoroughly understood either the systemic or pulmonary circulations, since he states that the veins carry the nourishment, as well as the arteries, to the viscera, and that the pulmonary arteries nourish the lungs. There can be no possible misunderstanding of Ruini's views as to the systemic circulation, as in his *Anatomy of the Horse*,<sup>1</sup> he says the vein that carries nutriment to the eye, and gives a

<sup>1</sup> Anatomia del Cavallo, in Venetia, 1599, Lib. i. p. 65.

figure illustrating this view. In speaking of the arteries and veins, we find that they appear to be made solely to carry nutriment to parts as noble as the spinal medulla; and they give nutriment, life, and motion to all these parts—a branch of the vein and artery. That Ruini had but an imperfect idea of the pulmonary circulation is evident from the manner in which he describes it, p. 108:

“The office of these ventricles is, for the right one, to prepare the blood, that the spirits of life can be generated from it and the lungs nourished; of the left to receive this blood already prepared, and to convert a part into spirits, which give life, and to send the rest, together with the spirits, by means of the arteries, to all parts of the body. In both the ventricles are two mouths or chinks; by that of the right the blood of the great vein, or cava, enters, and goes out by the arterial vein; by that of the left ventricle, the blood enters, accompanied by the air prepared in the lungs from the venous artery; this being entirely spiritualized and perfected in the left ventricle, goes out (guided by the great arteria) through all parts of the body, except that for the lungs, to impart it that heat which gives life.”

During the middle of the sixteenth century the fame of the medical schools of Italy had spread far and wide. Students from all parts of Europe crowded to listen to the eloquent lectures of Vesalius, Eustachius, and Fallopius, to attend the anatomical demonstrations given in the amphitheatres at Padua, Pisa, and Bologna. At the end of the sixteenth century, with other foreigners, William Harvey came to Padua and studied with the celebrated Fabricius, of Aquapendente, the first anatomist to describe thoroughly in his *De venarum ostiolis*, Patav, 1603, the valves in the veins.<sup>1</sup> Fabricius is often said to have first discovered these valves; indeed, he says so himself; but the presence of valves in the veins had been previously noticed by several anatomists; among others, by Cannanus,<sup>2</sup> Sylvius,<sup>3</sup> Eustachius,<sup>4</sup> and Piccolhominus.<sup>5</sup> At this moment, however, that which interests us particularly in reference to these valves is, that Fabricius demonstrated them to Harvey, and that the latter made such good use of that knowledge that the names of pupil and master have ever since been associated; for, undoubtedly, it was reflection upon what might be the use of the valves, as well as other anatomical considerations, that first led Harvey to investigate the manner in which the blood flows through the system. Harvey studied about five years at Padua (1598–1602). Naturally, during that time, he became thoroughly acquainted, not only with the views of his teachers, Fabricius, Rudio, etc., but also with those of Colombo, and probably of Cæsalpinus and others who had taught and written concerning the manner in which the blood was supposed to flow. Perfectly familiar with the anatomical views and methods of the school of Padua, dissatisfied with the prevailing imperfect

<sup>1</sup> Hieronymi Fabrici ab Aquapendente Opera Omnia Lipsiæ, 1687, De Venarum Ostiolis, p. 150.

<sup>2</sup> Amati Lusitani Medici Physici Præstantio Curationum Medicinalium, Lugduni, 1567.

<sup>3</sup> In Hippocrates et Galeni Physiologiæ partem anatomicam Isagoge a Jacobo Sylvio-Parisiis, 1555.

<sup>4</sup> Bartholmæi Eustachii Opuscula Anatomica Venetiis, 1584.

<sup>5</sup> Anatomiciæ Prælectiones Archangel Piccolhominii Romæ, 1586. By most writers the French anatomist, Etienne, is considered to have described the valves in the veins even before Cannanus or Sylvius. —De dissectione partium corporis humani libri tres a Carolo Stephano. Parisiis, 1545. Lib. ii. Hepar, Cap. ix. p. 182.



physiological theories of the circulation, on his return to England Harvey began anew the study of the flow of the blood. The results of his reflection upon the knowledge gained in Italy, of his studies upon his return, by numerous vivisections, of extended comparisons of the structure of the heart and bloodvessels in the animal kingdom, of pathological observations upon man and beast, were embodied in his classical treatise, *An Anatomical Exercise on the Motion of the Heart and Blood in Animals*.<sup>1</sup> This deservedly famous work will always serve as a model for physiological investigation. Thus Harvey shows the necessity of making vivisections<sup>2</sup> in the study of the circulation, and too much stress cannot be laid upon this statement, as it is often said that the circulation of the blood was discovered without recourse to experiments upon living animals. The importance of comparative anatomy as an aid to the study of physiology is well shown by the use that Harvey made of his knowledge of the structure and functions of the heart in the lower animals, in his researches upon the circulation. Indeed, Harvey says,<sup>3</sup> had anatomists only been as familiar with the dissection of the lower animals as they are with that of the human body, matters that have been a source of doubt would be free from all difficulty. Unfortunately, comparative anatomy is too much neglected by physiologists at the present day. That the value of pathological anatomy in throwing light upon the normal functions of the body was thoroughly appreciated by Harvey is evident from the cases he refers to<sup>4</sup> in connection with his study of the circulation. Harvey, therefore, did not confine himself to any one method of investigation, but availed himself of vivisection, comparative anatomy, and pathology in his researches. It may be seen by referring to the writings of the great predecessors of Harvey, that, with the exception of Cæsalpinus, it was always assumed that the venous blood flowed from the viscera to the periphery. Undoubtedly, Harvey demonstrated far more thoroughly, by experiment and argument, than Cæsalpinus, the true course of the venous blood, and this he proved in many different ways. Thus, in his thirteenth chapter,<sup>5</sup> after referring to the discovery of the valves of the veins by Fabricius, and the different uses that had been assigned to them, Harvey proceeds to show that the valves are disposed in such a way that they permit the blood to pass through them in only one direction, and that is toward the heart,<sup>6</sup> demonstrating this by calling attention, as Cæsalpinus had done before him, to the condition of the veins when compressed as if for bleeding. At intervals in the course of the veins, under such circumstances, large knots are visible, which are due to the distended valves, which thus show themselves externally. By pressing upon these veins above or below, or between the valves, Harvey showed that the venous blood always passed in the same direction—that is, toward the heart—and concluded that the functions of the valves were

<sup>1</sup> Exercitatio anatomica de motu cordis et sanguinis in animalibus. Francofurti MDCXXVIII.

<sup>2</sup> Op. cit., Cap. ii. p. 21; Cap. iv. p. 25.

<sup>3</sup> Cap. vi. p. 32.

<sup>4</sup> Cap. iii. p. 34.

<sup>5</sup> Cap. xiii. p. 54.

<sup>6</sup> It must not be forgotten that Piccolhominus had already described the valves in the jugular vein, and drew the conclusion that these valves prevented regurgitation to the head and extremities respectively. It is to be regretted that Harvey, in his description of the valves and the flow of blood through the veins, should never have mentioned either Piccolhominus or Cæsalpinus, as it is probable that he was acquainted with the writings of these anatomists, both teaching at Rome about the same time.

like those of the semilunar valves of the pulmonary artery and aorta, to prevent all reflux.<sup>1</sup> Excellent figures are given in this chapter to illustrate the experiments by which the functions of the valves were demonstrated. Further, that the blood flowed toward the heart in the veins and from the heart in the arteries, was beautifully demonstrated by an experiment upon a living snake, so clearly described by Harvey in Chapter X. After noticing the pulsating heart in the snake as it appeared after the animal had been opened, Harvey calls attention to the fact that if the vena cava be compressed it gradually empties itself between the point of compression and the heart; whereas, if the aorta be compressed, it becomes distended between the heart and the point of compression, showing conclusively that the blood in the vena cava flows toward the heart, while that in the aorta flows from the heart. In his second answer to Riolan, Harvey<sup>2</sup> gives further proof of the circulation in noticing that in a divided artery the blood flows from the end of the vessel that is still in connection with the heart, whereas, in the divided vein the blood flows from that part of the vessel separated from the heart. One of the most remarkable proofs of the circulation of the blood advanced by Harvey<sup>3</sup> is, that more blood passes through the heart in a given time than can be accounted for by the ingesta or by the quantity of the blood in the vessels; hence the blood must pass and repass through the heart, and in estimating the amount of blood flowing from the left ventricle into the aorta during a short period of time even, we necessarily count the same blood over and over again. Harvey was not only the first to describe correctly the entire circulation, but in the great work<sup>4</sup> we have so often referred to is found the first accurate account of the movements of the heart, the successive dilatations and contractions of the auricles and ventricles, the contraction, hardening, and elevation of the heart against the chest, etc. An excellent description, as may be supposed, is also given of the pulmonary circulation, etc. Further, though from the day of Aristotle it was known that there was some connection between the beating of the heart and the pulse, Harvey<sup>5</sup> showed clearly that the dilatation of the artery, or the pulse, was the effect of the contraction of the ventricle. Harvey was not the first, however, to show this, since in an ancient work, *Synopsis perī Sphugmon*, by an unknown author, the pulse in this respect was correctly described. When this work was first discovered, according to d'Aremberg, it was, without any reason, attributed to Rufus, of Ephesus. The description I refer to is to be found at page 20:<sup>6</sup>

“How is the pulse generated? The pulse is produced as follows: The heart, after having drawn in the air from the lung, first receives it in its left cavity, then falling back upon itself immediately distributes it

<sup>1</sup> The importance of the valves in the veins, either functionally or as leading to the discovery of the circulation, must not be exaggerated, since in many veins there are no valves. Thus in man, at least, however it may be in other mammals, valves are not found in the venæ cavae, the innominate, pulmonary, portal, hepatic, renal, uterine, ovarian, iliac, and spinal veins. Further, there are few valves in the veins of birds, reptiles, or fishes, and none in the veins of invertebrata, and yet the blood circulates in all these animals. It is evident, therefore, that the valves in the veins are not indispensable in the maintenance of the circulation.

<sup>2</sup> Opera Omnia Editā, 1766, p. 120. Exercitatio altera ad J. Riolanum.

<sup>3</sup> Cap. ix. p. 42.

<sup>4</sup> Cap. ii. iii. iv. v. vi.

<sup>5</sup> Cap. iii. p. 24.

<sup>6</sup> *Σύνοψις περὶ σφύγγων*, Traite sur le Pouls attribué a Rufus d'Ephese, par le Dr. Ch. Daremberg, Paris, 1846, p. 20.



to the arteries; it follows, then, that during the collapse of the heart, the arteries of the body being filled, their pulse is produced, and when empty, their systole. As I was saying, the pulse is produced in the arteries when full and receiving the air, and in the heart when empty, as we shall establish below."

In his view of the contraction of the ventricle being the cause of the dilatation of the artery, Harvey was anticipated also in modern times by Cæsalpinus, who observes<sup>1</sup> that "it happens that when the heart is contracting, the arteries are dilated, and it dilating, are contracted."

For, on account of the vessels ending in the heart, some pour their contents into this substance, as the vena cava into the right ventricle and venous artery (pulmonary vein) into the left; some draw out, as the arterial aorta, from the left ventricle, and the arterial vein (pulmonary artery), nourishing<sup>2</sup> the lungs from the right, but in all are valves placed and adapted to that use that their mouths, allowing to enter, do not lead out again, and those leading out do not allow to enter again; it so happens that, the heart contracting, the arteries are dilated, and dilating, contracted, not at once, as appears.

I might dwell further upon the numerous observations, demonstrations, and arguments based upon vivisections, comparative anatomy, pathology, etc., to be found in Harvey's work. The above brief descriptions will suffice, however, in giving an idea of the general methods of investigation and the results accomplished. The proofs advanced by Harvey were so numerous and convincing as to render the conclusion that the blood circulates inevitable. It was the only theory that would explain all the facts, the only view that enabled one to sift the truth from the error in the theories that had been advanced before Harvey's time. There is no doubt that Harvey was the first to teach that the blood flows from the right side of the heart through the lungs back to the left side of the heart, thence into the aorta and arteries throughout the body, from the arteries into the veins, returning by the veins to the heart again—in a word, that he was the first to describe thoroughly the entire circulation; but it must be admitted that he did not demonstrate it, for there is no reason to suppose that Harvey ever understood exactly, still less demonstrated, the manner in which the blood flows from the arteries into the veins, since the capillaries were not discovered till after his death.

With the discovery of the capillaries by Malpighi and Leeuwenhoek the entire circulation was for the first time demonstrated. That Harvey did not understand the manner in which the blood flowed from the arteries into the veins is evident from his own description. His words<sup>3</sup> are: "Signum est, etc., sanguinum ab arteriis in venas et non contra permeare et aut anastomosis vasorum esse aut porositates carnis et partium solidarum pervias sanguini esse"—that it "is obvious that the blood passes from the arteries into the veins, etc., and not the contrary; and that there are either anastomoses of the vessels or porosities of the

<sup>1</sup> *Questionum Peripateticarum*, 1593, Lib. Quint. Quest. iv. p. 122.

<sup>2</sup> It will be observed, from Cæsalpinus referring to the pulmonary artery being nutritive, that, as already mentioned, he did not understand the pulmonary circulation.

<sup>3</sup> Cap. xi. p. 48, *Secundum suppositum Confirmatur*.

flesh and solid parts that are pervious to the blood." Had Harvey ever seen the capillaries, or even had an idea of their structure, we may be assured that his description would have been a graphic one. There would have been no obscurity in reference to such an all important matter. That Harvey means by the word porositates, porosities or holes, and not capillaries, is evident from the way in which he uses this word in the introduction to the *Exercitatio*, where, in speaking of the theory of the ancients as regards the transmission of the blood through the septum of the heart, he says they hold "that there are numerous porositates in the septum of the heart, adapted for the transmission of the blood; but, by Hercules, there are no porositates, neither can they be demonstrated." If by porositates Harvey means capillaries, he would deny, then, that there are any capillaries in the septum of the heart. Harvey appears to me to use the word porositates just in the same sense (that of holes or porosities) as used, as we have seen, by De Carpi, Vesalius, etc., in the description of the septum of the heart. As regards the word anastomoses, Servetus and Cæsalpinus speak of the arteries passing into veins by anastomoses, and there is no more reason for supposing that Harvey understood by this word capillaries, than that they did.

For the discovery of the capillaries, in 1661, science is indebted to Malpighi.<sup>1</sup> In examining the lung of a living frog, by means of the microscope, this distinguished physiologist actually saw the blood passing from the arteries into the veins by means of extremely delicate tubes, at once the terminal branches of the arteries and the beginnings of the veins. These minute intermediate connecting tubes, the capillaries, were also seen by Malpighi in the mesentery of the living frog as well as in the lung. Some time after Malpighi's discovery, the capillary circulation was observed by Leeuwenhoek<sup>2</sup> (1688), the Dutch naturalist, with a microscope, in the lung of a bat, in the tadpole's tail, and in the fins of different kinds of fish. From that time forward, the magnificent spectacle of the capillary circulation became with microscopists a favorite subject for popular demonstrations. Between 1628, the epoch of the appearance of the *De motu cordis* of Harvey, and 1661, the year of the discovery of the capillaries by Malpighi, our knowledge of the circulation was extended by the discovery of the lacteals, etc. Obviously, without a knowledge of the lymphatic system, that of the circulation of the blood would be far from complete. In this connection, however, it will be only necessary to allude to the names of Eustachius, Aselli, Pecquet, Rudbeck, and Bartholinus, whose contributions to the discovery of the lymphatic system have already been referred to in the chapters treating of absorption. During the seventeenth century our knowledge of the exact manner in which the blood flows to all parts of the economy was greatly extended by the study of the vascular system, by means of injections. It is true this method of investigation had been occasionally attempted before this period, but with little success. It was not until Ruysch<sup>3</sup> had perfected the

<sup>1</sup> Marcelli Malpighi, *Opera Omnia*, Lug. Bat., 1687. Tomus secundus De Pulmonibus Epistola ii. p. 328.

<sup>2</sup> Arcan. Nat. Lugd. Bat., 1722, pp. 158, 163.

<sup>3</sup> For an account of Ruysch, see eulogy, by Fontenelle, in *Hist. de l'Acad. Sciences*, 1731, and Hyrtl, *Lehrbuch der Anatomie*, 1881, p. 61.



methods of Swammerdam and Horne, and had demonstrated, by his very perfect injections, the manner in which the bloodvessels are distributed through the tissues, that this method of study became universal with anatomists. It can readily be understood that when arteries, capillaries, and veins are filled with a colored injection, how much easier the course of these vessels can be made out, with either scalpel or microscope, than if these bloodvessels were simply studied in the state in which they are usually found in the body after death. Indeed, one of the most striking demonstrations of the continuity of the vascular system consists in injecting a fluid into an artery until the fluid escapes by an opening made in the vein. Further, during the seventeenth century, so fertile in discovery, the first attempts were also made in the study of the circulation of the invertebrata, Willis,<sup>1</sup> for example, describing the results of his researches upon the circulation of the oyster, lobster, etc. It is, however, only during the present century that physiologists have understood the circulation of the blood as it takes place in the mollusca, articulata, etc., the vascular system of animals, like insects, crabs, spiders, oysters, snails, etc., differing very much from that of man or the mammalia; Milne Edwards, more especially, having shown, among other peculiarities, for example, that the interorganic spaces or lacunæ play the part of bloodvessels in the invertebrata, as is the case in certain parts of the body of vertebrates also. Within the past twenty-five years great advances have been made in extending our knowledge of the circulation in other directions. Thus, by the introduction of the graphic method of study, we have seen, by means of kymographions, sphygmographs, cardiographs, etc., that we can determine blood pressure, the rapidity with which the blood flows in the system, etc., while the discoveries of Bernard, Brown-Séquard, Ludwig, etc., have shown us how local variations in the general circulation are due to the influence of the vasomotor nerves.

If our account has been a correct one, the history of the discovery of the circulation, recapitulated, divides itself naturally into a series of epoch-making periods—

1. The structure and functions of the valves of the heart. Erasistratus, B. C. 304.
2. The arteries carry blood during life, not air. Galen, A. D. 165.
3. The pulmonary circulation. Servetus, 1553.
4. The systemic circulation. Cæsalpinus, 1593.
5. The pulmonic and systemic circulations. Harvey, 1628.
6. The capillaries. Malpighi, 1661.

The history of the discovery of the circulation, like all other great movements, social, political, and scientific, illustrates the profound truth that intellectual development is as surely a growth regulated by law as the life of a plant or animal. That no intellect, however magnificent, rises so above the conditions of its environment as to make it doubtful, for a moment, that the discovery would have been made sooner or later, even had the name with which it is usually associated, never existed. Every mind is the product of its age. All the circum-

<sup>1</sup> Willis's Works, translated by S. Pordage, London, 1684: Of the Soul of Brutes, Chap. iii. pp. 10, 11, Tables ii. iii.

stances prove that intellectual Europe at the end of the sixteenth century was ready to accept the circulation of the blood. Had the discovery been made some centuries sooner it would have fallen still-born. All Italy, at that period, was alive with speculation, hypothesis, theory, as to the manner in which the blood flowed through the body, and above all, Padua. Let anyone compare the works of the great Italian anatomists and physiologists of the sixteenth century, in their Latin or Italian dress, with the admirable work of Harvey on the circulation, in the original, and not in an English translation, and he will be impressed with the fact that the same mode of thought and expression pervades both. In his methods of investigation, observation, and arguments, Harvey is essentially Italian. By birth an Englishman, in thought Italian, Harvey lived and died a student of Padua.

The discovery of the circulation of the blood, as we learn from this necessarily brief account, belongs, therefore, to no one age, country, or person. Its history, extending as it does over a period of more than 2000 years, naturally suggests that the subject would have attracted the attention of the great medical minds of all time; and such we have seen was the case. Far from the grandest generalization in the whole range of biology being discovered in its entirety by one mind, we have seen how, little by little, it was gradually established by many observers; that long intervals would elapse without any progress being made, when suddenly some ancient error would be dissipated and fade away in the light of advancing science. Such a history ought to encourage every student, for however trivial and unimportant his experiments or observations may appear at the time, every new fact once well established will sooner or later assume its appropriate place as a part of some future generalization; the chain of facts leading to a great discovery being united together like living things, each linked with those that have passed away with those still to come. Discoveries great in themselves have often borne no fruit at the time, falling on barren soil, the human mind not being sufficiently developed to appreciate them. With the progress of knowledge, however, the significance of discoveries made often ages ago and long forgotten, become, in time, apparent to all. Truth, like the rays of the rising sun, is perceived first by those whose minds soar above the intellectual horizon of their day, but sooner or later its genial influence is felt by their humble followers, by all alike, all in good time.



## CHAPTER XXVI.

### RESPIRATION.

WE have seen that all vital activity is accompanied by waste, that mental, muscular, and secretory action, and the production of animal heat, involve the development of carbonic acid, urea, etc. Such principles produced through the decomposition of the food and tissues, if retained in the system soon cause death, hence the necessity of their being eliminated; excreted. As the degree of vital activity is conditioned by that of the cell, of fermentation, oxidation, etc., and as it is through respiration that oxygen is absorbed, and carbonic acid exhaled, it is evident that this function is both absorbing and excretory in character, and must constitute a most important part of nutrition. As might be expected, therefore, the absorbing of oxygen and elimination of carbonic acid are not necessarily limited to any part of the body, but may go on in every part of it. Further, while the carbonic acid excreted is, to a considerable extent, due to the combination of the oxygen absorbed with the carbon of the body, there is no reason to suppose that the carbonic acid excreted at any one moment is produced through the combustion of the oxygen supplied by the air inspired at that moment. On the contrary, the oxygen may have been locked up in the tissues, and supplied, not from the lungs, but from a different part of the economy altogether. In fact, an animal will exhale carbonic acid in an atmosphere of hydrogen. Under such circumstances, the oxygen of the carbonic acid must have been absorbed at some previous period.

In the widest sense of the term respiration may then be considered as the process by means of which oxygen is absorbed by the system, and carbonic acid is excreted, whatever may be the source of the latter. It is often said that, while animals inhale, plants exhale oxygen, and that animal and vegetable life stand, therefore, in a complementary relation to each other. In one sense this is true, since green plants under the influence of solar light decompose carbonic acid and water, giving up the oxygen and appropriating the carbon, elaborating the latter into starch, fat, cellulose, etc. Animals, on the other hand, through the absorption of oxygen, burn the carbon of their food produced by plants, and exhale carbonic acid. This antithesis between plant and animal life exists only so long as the plant is regarded as the means by which inorganic matter is combined in a form suitable as nutriment for the animal. When, however, the remaining phenomena of plant life are considered, such as the germination of the seed, the expansion of the leaf, the budding and flowering, the movement of the sap, it will be found that all such depend upon the absorption of oxygen, and cease when the plant is deprived of it. Respiration, therefore, is as important a function in plant as in animal life.

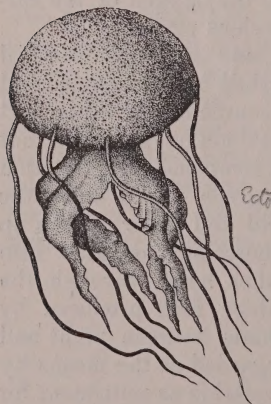
The phenomenon of respiration or breathing in animals is usually associated with the presence of specialized organs, like lungs, gills, etc. Such structures are, however, not indispensable for the performance of this function, since the muscle of a frog, when separated from the animal and drained of its blood, will absorb oxygen and excrete carbonic acid as long as the muscle retains its irritability. There are, indeed, two kinds of respiration, an internal one, taking place in all parts of the body, the tissues giving up to the blood the carbonic acid generated in them, and absorbing oxygen from it, and an external one, the blood giving up to the atmosphere through the lungs or skin its carbonic acid and receiving oxygen. It is the latter form, or external kind of respiration, ordinarily known as breathing, that we propose considering more particularly at present.

A respiratory organ consists essentially of a membrane separating tissue or blood, containing carbonic acid, on the one hand, from the atmosphere, or some other medium containing oxygen, on the other; the membrane being of such a character as to permit of osmosis.

As an interesting illustration of the osmosis of the carbonic acid of the blood and oxygen through animal membrane may be mentioned the experiment performed more than fifty years ago by our late colleague, Prof. R. E. Rogers, in which a fresh pig's bladder having been filled with venous blood, and enclosed in a bell glass of oxygen, a large quantity of carbonic acid left the blood and passed through the membrane; while, on the other hand, a quantity of oxygen disappeared, having passed through the membrane in the reverse direction into the blood.

Whether the animal be aquatic or terrestrial, simple or complex, the respiratory organs are only modifications of this simple membranous

FIG. 209



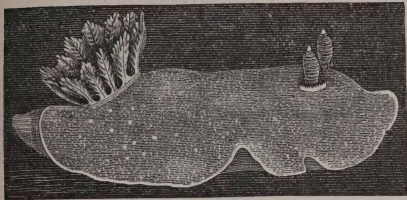
Jelly fish. (MILNE EDWARDS.)

type of structure, and this will be found to be true, as they appear in the form of skin, gills, tracheæ, or lungs. Thus, in many of the lower forms of life, as in the hydrozoa and actinzoa, of which the jelly fish (Fig. 209) and anemone are familiar examples, are simply formed animals, in which the differentiation of the functions, or the division of labor is not carried to any great extent, respiration is effected by the general cutaneous surface, the ectoderm or skin readily permitting an exchange between the oxygen dissolved in the sea-waters and the carbonic acid developed within their bodies. In the star fish, sea urchin, and echinodermata generally, respiration, while still chiefly cutaneous, is, to a certain extent, localized, the ambulacral suckers or feet acting probably also as respiratory organs. In the holothuroidea, also echinodermata, which, from their fancied resemblance to cucumbers, are popularly known at the sea shore by that name, respiration is still more specialized, being effected by an arborescent-like organ, a growth or diverticulum from the terminal



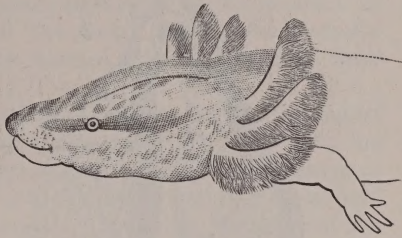
portion of the alimentary canal, which dividing and subdividing tree-like, reaches to the anterior portion of the body. This structure, floating freely in the visceral cavity, can, at the will of the animal, be

FIG. 210.



*Doris Johnstonei*, showing the tuft of external gills.  
(CARPENTER.)

FIG. 211.



Head and gills of menobranchius. (DALTON.)

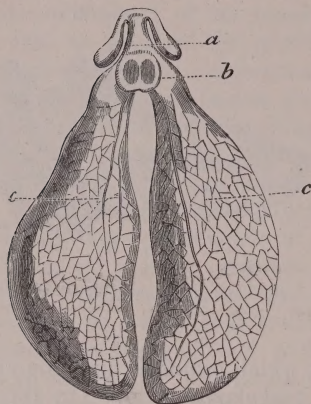
filled through the anus with sea-water, which osmosing into the visceral cavity passes thence into the water vascular system. On the other hand, the respiratory organs, in many animals, assume the form of gills, delicate membranous-like structures, whose thin walls readily permit of an osmosis between the oxygen of the surrounding water and the carbonic acid of the blood circulating within. Such a type of respiration obtains in the mollusca, of which the oyster, scallop, cuttle-fish, and doris (Fig. 210) are examples; in fishes, the perennibranchiate batrachia (Fig. 211).

Another form of respiration is the tracheal. This is seen in insects, centipedes, etc., and consists of innumerable delicate membranous branching tubes, ramifying throughout the entire body of the animal, and opening externally by usually lateral apertures the spiracles or stigmata; between the layers of which the tracheæ consists is inclosed a spirally convoluted fibre, to which is due their strength and flexibility. The air enters by the spiracles or openings, and is conveyed by the tracheæ, or breathing tubes, to all parts of the system. Finally, in batrachia, reptiles, birds, and mammals, including man, respiration is effected by the skin and lungs. The action of the skin as a respiratory surface will be considered with the other functions of that structure, and in describing the lungs in man, let us begin with a more simple type of lung than that of the frog, for example.

The lungs of the frog (Fig. 212) consist of two vascular bladder-like sacs, communicating directly by short bronchi, or rather bronchial openings, with the larynx. On opening the lung the inner surface (Fig. 213) will be seen to be more or less honeycombed, and the alveoli subdivided into still smaller spaces, or cells. These cells all communicate with the central pulmonary cavity, and are lined with a capillary network intermediate between the arterioles running along the attached borders of the septa and the venules along the free borders. It is evident that a far greater extent of vascular surface is exposed to the air, by this segmented or honeycombed disposition of the inner surface, than if the latter was smooth. If the lungs of the frog be now compared with

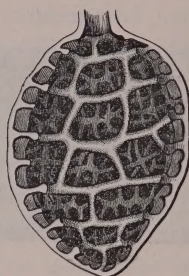
those of a lizard or turtle, the only noticeable difference is that this segmentation of the lung is more marked, while in birds and mammals it

FIG. 212.



Respiratory organs of a frog, as seen on their anterior surface. *a.* Hyoidean apparatus. *b.* Cartilaginous ring at the root of the lungs. *c.* Pulmonary sacs, covered with vascular ramifications. (CARPENTER.)

FIG. 213.



Lung of frog, showing its internal surface.  
(DALTON.)

is carried to such an extent that each lung consists essentially of an immense number of these honey-combed sacs, subdividing into cells, the extent of the vascular surface exposed to the air being enormously increased. When we come to study development we shall see that the lungs in mammals begin as buds or sac-like diverticula of the œsophagus, which soon segment. In this transitory condition the lungs of the mammalian embryo are comparable to those of the frog. As development advances this segmentation continues until the bronchus, instead of opening into one pulmonary sac, as in the frog, through its division into bronchial tubes, opens into an innumerable number. The ultimate sacs are then known as pulmonary lobules, and the little honeycombed spaces as air cells. A lobule of the mammalian lung acts, therefore, like the whole lung of the frog, the only difference being that it is smaller, the air cells in one being seen only by aid of the microscope, in the other being perfectly visible to the naked eye.

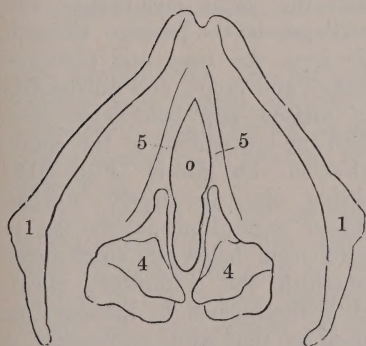
It is worthy of mention that the frog at different periods of its existence breathes by skin, gills, and lungs, and that the transitory stages through which its respiratory organs pass are permanently retained in the lower forms of life. The respiratory organs in man, in the widest sense of the term, include the nares, mouth, pharynx, larynx, trachea, lungs, thorax, and appropriate muscles. That the nares, not the mouth, constitute the natural entrance for the air to the lungs is shown by the fact that in certain mammals breathing is accomplished through the nares alone. Thus in the cetacea, of which the whale, dolphin, porpoise, etc., are examples, the soft palate is very much developed and so disposed to embrace the glottis and maintain the cavity of the larynx in communication with the posterior nares, a free passage way, however, being left on either side for the food. Such a disposition of the parts makes it possible for the elephant to use its



nose or trunk, pharynx and larynx as a siphon to suck up its drinks and transfer the same to the mouth, at the moment that the latter is open the posterior nares communicating with the glottis only. In the horse, camel, etc., the soft palate is also well developed, and surrounds the large epiglottis to such an extent as to cut off completely all communication between the mouth and pharynx, except at the moment of deglutition. Indeed, in the horse, if the facial nerves which supply the muscles of the external nares be divided, the animal dies from asphyxia.

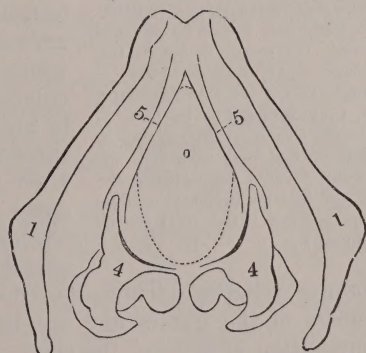
In describing the structure of the hippopotamus, the author called attention<sup>1</sup> to the fact that when the animal passes under the water, the larynx is so elevated within the pharynx that a continuous passage is offered to the air from the external nares to the lungs, enabling the animal to breathe when almost entirely submerged. A similar elevation of the larynx is seen in the young kangaroo, and to a certain extent, also, in the human foetus and infant. The ill effects often experienced in breathing through the mouth in a cold, dry atmosphere further prove that the natural entrance to the respiratory tract is the nose, since the air as it passes over the partly ciliated moist and very vascular and warm mucous membrane lining the nasal cavities absorbs water, and is elevated to the temperature of the body before entering the lungs. The action of the nares in ordinary breathing is not very apparent, but when the breathing becomes labored, then it is very evident. The air having passed the nose and the pharynx, enters the larynx, a triangular-like structure surmounting the trachea and consisting of

FIG. 214.



Human larynx, viewed from above in its ordinary post-mortem condition. 5. Vocal cords. 1. Thyroid cartilage. 4. Arytenoid cartilages. 0. Opening of the glottis. (DALTON.)

FIG. 215.



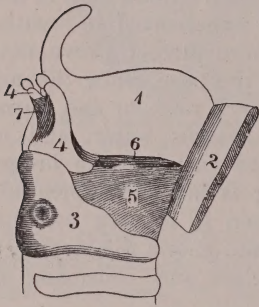
The same, with the glottis opened by separation of the vocal cords. 5. Vocal cords. 1. Thyroid cartilage 4. Arytenoid cartilages. 0. Opening of the glottis. (DALTON.)

sufficiently rigid cartilage to resist atmospheric pressure, united by ligaments and movable through muscles. The detailed structure of the larynx we will defer till our account of the voice, considering at

<sup>1</sup> Proc. Acad. Nat. Sciences, p. 130. Philadelphia, 1881.

present only such of its parts as influence respiration. The larynx is lined with mucous membrane, continuous with that of the pharynx; the epithelium, however, except that covering the vocal cords, is of the ciliated, columnar variety, the movement of the cilia being from below, upward. If the larynx be viewed from above (Figs. 214, 215), or in section (Fig. 216), it will be observed that it is divided into an upper and lower compartment by the rima glottidis (0), or the aperture of the glottis, a triangular-like orifice, the sides and base of which are formed by the true vocal cords (Figs. 214, 216) (5, 5) and arytenoid cartilages (4). The vocal cords, or, more properly, the vocal membranes, consist of elastic tissue covered with very thin mucous membrane, and extending from the thyroid cartilages (Fig. 216, 1 and 2), anteriorly to the cricoid (3), and base of the arytenoid cartilages (4) posteriorly. The upper edges of the vocal membrane extending from the reëntering angle of the thyroid cartilage to the base of the arytenoid are somewhat thickened, and are usually and incorrectly described as separate organs, the "vocal cords." The upper or false vocal cords, so-called because they have no influence in the production of voice, are the thickened upper edges of the ventricle or sac-like pouches extending outward and upward from the larynx between the vocal cords, and lined with the mucous membrane of the same. The glottis or triangular orifice between the vocal membranes and arytenoid cartilages is the passage through which the air from the nose and pharynx enters the trachea and lungs, and during life is alternately dilated and contracted synchronously with the movements of the chest. During inspiration the glottis (Fig. 215) opens, admitting the air freely to the trachea, while in expiration as the air is expelled upward from below, the vocal membranes collapse. These movements constitute the respiratory movements of the glottis and are increased or diminished in intensity in proportion to those of the chest. We shall see that while expiration is usually a passive process, inspiration is an active one, and its tendency is to draw the vocal membranes together. This is provided against, however, through the action of the posterior crico-arytenoid muscles, which arise from the posterior surface of the cricoid cartilage converge upward and outward, and are inserted into the base of the arytenoid cartilages. In contracting, these muscles, therefore, dilate at the moment of inspiration the glottis. During expiration, however, these muscles are relaxed, the vocal membranes through their elasticity, and through the contraction of the lateral crico-arytenoid muscles are approximated, and the expired air separates them as it passes upward

FIG. 216.



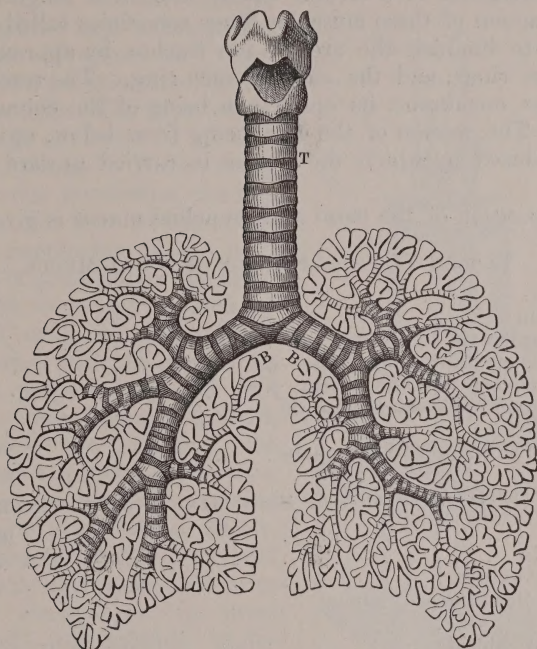
View of the vocal membrane. 1. Left half of the thyroid cartilage. 2. Right half turned forward and partly cut away. 3. Cricoid cartilage. 4. Arytenoid cartilages. 5. Right half of the vocal membrane. 6. Upper border of the left half. 7. Arytenoid muscle. The upper borders of the vocal membrane, extended between the arytenoid cartilages and the thyroid, constitute the so-called "true vocal cords." (LEIDY.)

During inspiration the glottis (Fig. 215) opens, admitting the air freely to the trachea, while in expiration as the air is expelled upward from below, the vocal membranes collapse. These movements constitute the respiratory movements of the glottis and are increased or diminished in intensity in proportion to those of the chest. We shall see that while expiration is usually a passive process, inspiration is an active one, and its tendency is to draw the vocal membranes together. This is provided against, however, through the action of the posterior crico-arytenoid muscles, which arise from the posterior surface of the cricoid cartilage converge upward and outward, and are inserted into the base of the arytenoid cartilages. In contracting, these muscles, therefore, dilate at the moment of inspiration the glottis. During expiration, however, these muscles are relaxed, the vocal membranes through their elasticity, and through the contraction of the lateral crico-arytenoid muscles are approximated, and the expired air separates them as it passes upward



from the trachea. The importance of the epiglottis covering the larynx during deglutition, and thereby preventing foreign bodies, especially

FIG. 217.

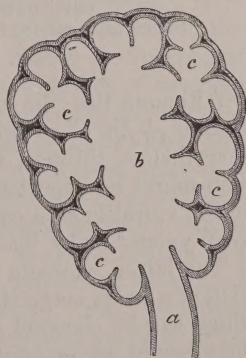


Human larynx, trachea, bronchi, and lungs; showing the ramification of the bronchi, and the division of the lungs into lobules. (DALTON.)

of a liquid nature, from passing into the larynx having been already noticed, it will not be necessary to dwell further upon the function of this structure in its relation to deglutition and respiration.

The inspired air having passed through the larynx enters the trachea (Fig. 217, T), a tube from 10 to 12 cm. long (4 to  $4\frac{1}{2}$  in.), and  $\frac{1}{3}$  cm. ( $\frac{3}{4}$  in.) in width, beginning at the lower border of the cricoid cartilage above and terminating as the two bronchi below. The trachea consists of 16 to 20 cartilaginous rings, or, more correctly, in the form of arcs the posterior third of each ring being imperfect, deficient in cartilage, the intervening space being filled up with loose fibrous tissue. The cartilaginous rings are connected by a strong fibro-elastic membrane, which so extends over and under them in a thinned condition that they are, as it were, imbedded within it. The last ring of the trachea is somewhat modified in shape, its lower border being brought

FIG. 218.



Single lobule of human lung. *a* Ultimate bronchial tube. *b*. Cavity of lobule. *c, c, c*. Pulmonary cells, or vesicles. (DALTON.)

The last ring of the trachea is somewhat modified in shape, its lower border being brought

to a median point so as to accommodate itself to the bronchi. Within the fibrous tissue filling up the posterior third of the cartilaginous rings are found unstripped muscular tissue, the fibres of which are disposed in a transverse, and to a certain extent, also in a longitudinal direction. The action of these muscular fibres sometimes called the tracheal muscles, is to diminish the area of the trachea by approximating the cartilaginous rings, and the ends of each ring. The trachea is lined with mucous membrane, its epithelium being of the columnar ciliated character. The motion of the cilia being from below, upward, a current is produced by which the mucus is carried upward toward the larynx.

The composition of the nasal and bronchial mucus is given in :

TABLE LVI.<sup>1</sup>—COMPOSITION OF NASAL MUCUS.

|                                          |        |
|------------------------------------------|--------|
| Water . . . . .                          | 993.00 |
| Mucosin . . . . .                        | 53.30  |
| Sodium lactate . . . . .                 | 1.00   |
| Organic crystalline principles . . . . . | 2.00   |
| Fatty matters and cholesterin . . . . .  | ....   |
| Sodium and potassium chloride . . . . .  | 5.60   |
| Phosphates . . . . .                     | 3.50   |
| Sodium sulphate and carbonate . . . . .  | 0.90   |

TABLE LVII.<sup>2</sup>—COMPOSITION OF BRONCHIAL AND PULMONARY MUCUS.

|                                                 |         |
|-------------------------------------------------|---------|
| Water . . . . .                                 | 955.520 |
| Mucosin . . . . .                               | 23.754  |
| Watery extract . . . . .                        | 8.006   |
| Alcoholic extract . . . . .                     | 1.810   |
| Fat . . . . .                                   | 2.887   |
| Sodium chloride . . . . .                       | 5.825   |
| “ sulphate . . . . .                            | 0.400   |
| “ carbonate . . . . .                           | 0.198   |
| “ phosphate . . . . .                           | 0.080   |
| Calcium phosphate with traces of iron . . . . . | 0.974   |
| “ carbonate . . . . .                           | 0.291   |
| Silica and calcium sulphate . . . . .           | 0.255   |
| <hr/>                                           |         |
| 1000.000                                        |         |

Although the cilia are microscopic, varying in length from the  $\frac{1}{160}$ th to the  $\frac{1}{160}$ th of a mm. (the  $\frac{1}{2500}$ th to  $\frac{1}{4000}$ th of an inch) in length; nevertheless, through their vibratory motion a greater force is exerted than might be expected. The mechanical effect produced by the motion of the vibratile cilia can be shown by means of the instrument devised by Wyman,<sup>3</sup> or by that of Calliburces.

The latter, as made for the author by Aubrey, of Paris, consists (Fig. 219) of a brass stage H, 11 cm. long and 7 cm. wide (4.5 and 3 inches), which can be elevated and depressed on a vertical axis (K) by means of the screw M, whose movement is graduated. The brass stage supports a cork (I) 5 cm. long and 3 cm. wide (2 and 1.2 inches), and the vertical axis L, an aluminium rod, 5 cm. long (2 inches) and with a diameter of 1.5 mm. (1.25th of an inch) horizontally disposed, and terminating in

<sup>1</sup> Robin : Leçons sur les humeurs, p. 450. Paris, 1867.

<sup>2</sup> Nasse : Journal of prakt. Chemie, 1843, Band xxix. S. 65.

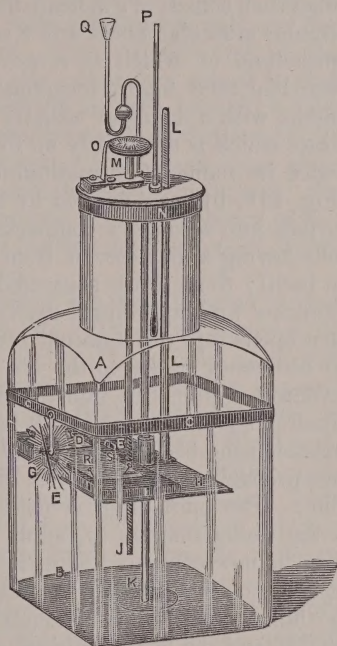
<sup>3</sup> Experiments with vibrating cilia, American Naturalist, vol. v. p. 611, 1871.



an index (F) and partly surrounded by glass. The vertical index (L) is surmounted by a brass disk N, through which passes a safety tube into which hot water can be poured, by means of which the surrounding atmosphere can be kept moist, and at a temperature of about  $28^{\circ}$  Cent. ( $82^{\circ}$  Fahr.), and a thermometer (P) for indicating the same. The brass stage, axis, and disk, etc., can be covered with a glass cylinder. Before doing this, the mucous membrane, the motion of whose cilia is to be examined, that of the oesophagus of the frog, for example, is placed upon the cork, and the brass stage (H) elevated by the screw (M) until the membrane is almost in contact with the aluminium rod. When properly adjusted, and the membrane kept moist and warm by the means just indicated, the aluminium rod will rotate on its axis, the index at its end (F) moving over the graduated brass circle, having a diameter of 2.6 cm. (1.04 inch). Usually the index will move around the circle once in three minutes, and the motion, under favorable circumstances, will continue for an hour and upward. As the aluminium rod, with the glass surrounding it, and the index weigh about 0.073 gr. (1.05 grain), it is evident that considerable mechanical effect is produced relatively to the small size of the organs exerting the force. The motion of the cilia of human mucous membrane can often be seen upon the surface of recently extracted nasal polypi when the latter are viewed under the microscope.

The trachea terminates inferiorly in the bronchi (Fig. 217, B); the right bronchus, differs from the left in being the shortest, attaining, usually, a length of 2.5 cm. (1 inch), while the left is almost twice as long. The general structure of the bronchi corresponds in every way to that of the trachea; the cartilaginous rings are, however, shorter and narrower, and less numerous, the right bronchus consisting, usually, of from six to eight rings, the left of from nine to twelve. Each bronchus divides and subdivides dichotomously into the bronchial tubes (Fig. 217). The latter, diverging in every direction, and never anastomosing, gradually become smaller and smaller, and more delicate in structure, and when, finally, they are reduced to about a diameter of the  $\frac{1}{5}$ th of a mm. ( $\frac{1}{120}$ th of an inch), they terminate in a primary lobule (Fig. 218). The bronchial tubes differ in several respects from the bronchi, of which they are the diverging branches. Thus, in the larger ones, the cartilages are disposed as irregular-shaped plates, of various sizes, all over

FIG. 219.



Apparatus of Calliburcès.

the sides of the tubes instead of in the form of imperfect rings; in the medium-sized tubes the cartilages become smaller and less numerous, while, finally, in tubes having a diameter of less than  $\frac{1}{2}$  of a mm. ( $\frac{1}{50}$ th of an inch) they disappear altogether. The terminal bronchial tubes then consist of a delicate fibro-elastic external membrane, containing circular muscular fibres and a very thin lining of mucous membrane, the epithelium of which is, however, still ciliated. As just stated, each bronchial tube finally terminates in a primary lobule. The primary lobule, with a diameter usually of 2 mm. ( $\frac{1}{12}$ th of an inch), consists of a sac, which is essentially an expansion of the terminal bronchial tube, hence its name of infundibulum. The cavity of the primary lobule (Fig. 218, b) is subdivided by thin partitions, projecting from its inner surface into secondary compartments, or alveoli *c*, the pulmonary air cells having a diameter of from  $\frac{1}{8}$ th to  $\frac{1}{3}$ d of a mm. ( $\frac{1}{200}$ th to  $\frac{1}{75}$ th of an inch); these, while separated from each other by the partitions, communicate with the central cavity or intercellular air passages, which, in turn opens into the terminal bronchial tube, through which the inspired air ultimately passes to the air cells. The air cells, amounting to over seventeen millions in number, and representing an area of nearly two hundred square metres (1800 feet), are polyhedral sacs, surrounded by anastomosing elastic fibres, and consist of a fibro-elastic wall, containing, probably, some muscular fibres, and lined with a tessellated epithelium. The epithelium is more homogeneous and easily demonstrated in the foetus than in the adult. If the primary lobule of the human lung be now compared with the lung of the frog, it will be seen that it represents the entire frog's lung in miniature. The primary lobules of the human lung unite through connective tissue into larger secondary lobules, and the latter, uniting, constitute a lung. The polyhedral markings upon the surface of a lung indicate the margins of the secondary lobules, while careful examination will disclose also the outlines of the

FIG. 220.

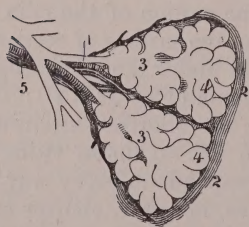


Diagram of two primary lobules of the lungs, magnified. 1. Bronchial tube. 2. A pair of primary lobules connected with fibro-elastic tissue. 3. Intercellular air passages. 4. Air cells. 5. Branches of the pulmonary artery and vein. (LEIDY.)

primary lobules composing the secondary ones. Finally, the integration of the primary lobules into the secondary ones, and the latter into lobes, carried still further into the left lung than in the right, the former consisting of two lobes, the latter of three. While the lungs are nourished by the bronchi, it is by means of the pulmonary arteries that the venous blood is carried to them from the right side of the heart and aerated. The pulmonary artery arising, as we have seen, from the right ventricle of the heart, soon divides into a right and left branch for either lung. Following the bronchus and bronchial tubes, the artery divides and subdivides, the branches becoming smaller and smaller as they approach the primary lobules (Fig. 220), until finally they terminate as the pulmonary capillaries. The terminal arterial capillaries surround each alveolus or air cell as a vascular circle, which anastomoses



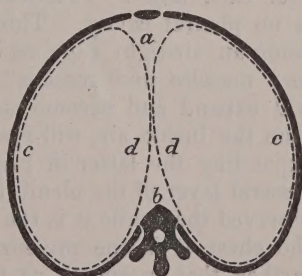
with those of the adjacent alveoli. From these vessels arise a capillary network (Fig. 220), so closely set that the meshes are even smaller than the diameter of the vessels themselves, the latter having usually a diameter of from  $\frac{1}{80}$ th to  $\frac{1}{200}$ th of a mm. ( $\frac{1}{2000}$ th to  $\frac{1}{5000}$ th of an inch). This network supports the bottom of each air cell, and the blood that it carries is separated from the air of the cells only by its wall and the extremely delicate epithelial lining of it. The carbonic acid of the venous blood conveyed to the lungs by the pulmonary artery is thus separated from the oxygen of the air within the air cells brought by the trachea by nothing but the wall of the capillary and epithelium of the air cell. The rapidity with which the osmosis of these gases takes place through such a delicate septum will, therefore, be readily imagined; the osmosis being still further insured through the great vascularity of the parts, the respiratory surface being thereby continually kept moist, which greatly promotes the exchange of the gases.

The full influence of the air upon the blood is further secured in that the capillary plexus is so disposed between the walls of two adjacent air cells that one of its surfaces is exposed to each. It has been estimated<sup>1</sup> that a thin layer of blood of 150 square metres (1350 feet) is exposed in the lungs to the air of the air cells, and that this blood, amounting to perhaps 2 litres (4 pints), is renewed 10,000 times in twenty-four hours. This estimate is based upon the assumption that the surface of the capillaries is equal to about three-fourths the surface of the air cells. That this is not an exaggeration may be inferred from the fact of an injected lung appearing to consist of nothing but capillaries. From the capillary network surrounding the air cells the pulmonary veins arise, which, uniting with each other, gradually form four larger trunks, which finally terminate in the left auricle of the heart and convey to it the aerated oxygenated blood to be distributed, as we have seen, by the arterial system to all parts of the body.

Having described the pulmonary air cells and bloodvessels, the passage by osmosis of the carbonic acid from the blood into the air cells and of the oxygen from the air cells into the blood, let us now consider the means by which the external air is drawn into the lungs and the carbonic acid expelled from them.

The heart and lungs are suspended by the great bloodvessels in the thoracic cavity. The thorax consists of the sternum anteriorly, the dorsal vertebra posteriorly, and the ribs laterally. It is covered in above by the cervical muscles and fascia, below by the diaphragm, and laterally, etc., by the intercostal muscles. The thoracic cavity is therefore air-tight. If the lungs be examined *in situ* it will be found that the surface of each lung is covered with a serous membrane continuous with that lining the inner surface of the thorax or the pleura.

FIG. 221.



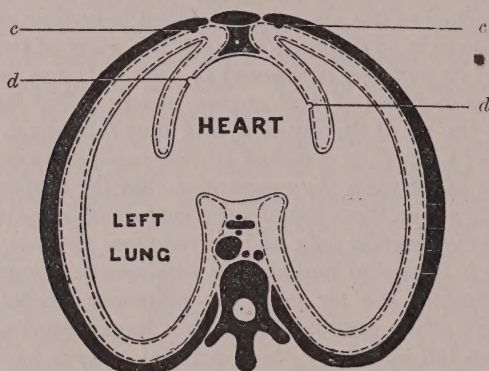
Diagrammatic view of pleural sacs.

<sup>1</sup> Kuss: Physiologie, 1873, p. 338.

To understand the relations of the pleura to the lungs and walls of the thorax, let us first conceive the pleura as consisting of two bladders (Fig. 221), and so placed within an empty thorax that the outer wall (*c*) of each bladder will adhere to the inner wall (*b*) of the thorax, the inner walls (*d*) of each bladder remaining free.

Suppose now that the heart and lungs be inserted between the inner free walls of the two bladders, and that each of the latter be made to adhere to the surface of the lung with which it is in contact. Such a disposition being made (Fig. 222), the bladders will then represent the two pleura; the inner walls (*d d*) the visceral layer, the outer wall (*c c*) the parietal layers, and the space between the layers the pleural cavities, the spaces between the bladders or the pleura constituting the mediastinal spaces, the narrow septum formed through the union of the

FIG 222.



Diagrammatic view of pleural sacs with heart and lungs interposed.

two pleura the mediastinum. In health the opposed surfaces of the visceral and parietal layers of the pleura are always in contact, there being only fluid enough between them to insure their gliding smoothly over each other. Practically, therefore, in normal respiration there is no pleural cavity. This must necessarily be so, since the thorax being an air-tight cage, as it dilates through the action of the inspiratory muscles and recedes from the lungs, the air within the latter will expand and become rarefied; the external air being then denser than the inside air, will rush through the trachea into the lungs, and expanding the latter in proportion as the thorax is dilated, keep the visceral layer of the pleura in contact with the parietal one. It will be observed that while it is the force of the inspiratory muscles that dilates the chest, it is the pressure of the air that expands the lungs, and, further, that inasmuch as the lungs are elastic and therefore offer a resistance to their expansion, the air must overcome this resistance, and hence the pressure exerted by the air within the lungs during inspiration must be less than that of the external atmosphere. The significance of this fact we shall see shortly. On the other hand, as the thorax contracts as its capacity diminishes, the air within the lungs exerting now



a greater pressure than the air without, will pass out of the lungs, through the trachea by which it had just entered, the lungs, of course collapsing, their elasticity now aiding the expulsion of the air to the same extent as it formerly opposed its entrance. The dilatation of the thoracic cavity and the taking in of the air is known as inspiration, the contraction of the thoracic cavity and the giving out of the air expiration, the two acts constituting respiration.

Let us consider now a little more in detail the means by which this alternate dilatation and contraction of the thoracic cavity causing respiration is effected.

## CHAPTER XXVII.

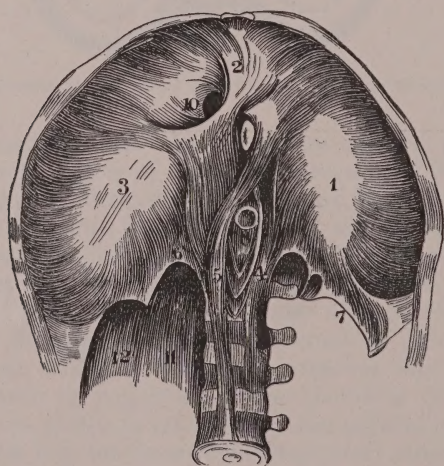
### MUSCLES OF RESPIRATION.

REFLECTION upon the origin and insertion of the various muscles acting upon the thorax makes it evident that some of these muscles in contracting will expand the chest, causing inspiration, while the relaxation of these muscles together with the elasticity of the lungs and the action of certain other muscles, will contract it, causing expiration. The muscles involved in the production of respiration will then naturally divide themselves into two groups, those of inspiration and those of expiration (Table LVIII., page 410). To the study of these let us now turn.

#### INSPIRATION.

Of all the inspiratory muscles the diaphragm is the most important, since the capacity of the chest is enlarged to a greater extent through its contraction than by that of any other muscle. Indeed, in the male sex at least, as we shall see, gentle breathing is accomplished

FIG. 223.



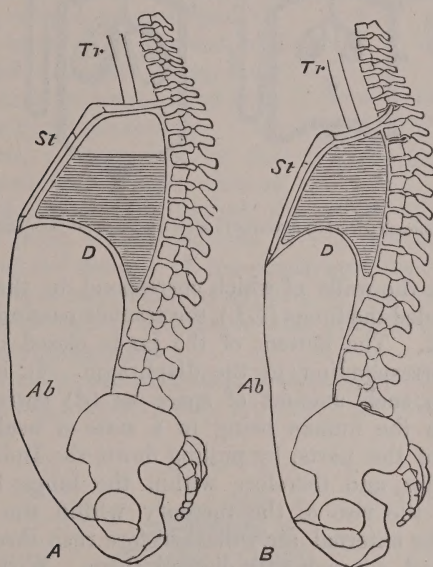
Interior view of the diaphragm. 1, 2, 3, the three lobes of the central tendon, surrounded by the fleshy fasciculi derived from the inferior margin of the thorax, the crura, 4, 5, and the arcuate ligaments, 6, 7; 8, aortic orifice; 9, oesophageal orifice; 10, quadrate foramen; 11, psoas muscle; 12, quadrate lumbar muscle.

almost entirely by the action of the diaphragm. The diaphragm (Fig. 223), arising from the ensiform cartilage of the sternum, the cartilages of the six or seven lower ribs, and often, also, from their



osseous portions from the arcuate ligaments and the bodies of the first, second and third lumbar vertebræ, and the intervertebral cartilages of the right side, and from the bodies of the first and second lumbar vertebræ, etc., of the left, or the cruræ, covers in therefore the lower circumference of the thorax. From this origin the diaphragm passes upward into the cavity of the thorax as a vaulted arch or dome (Fig. 224, *B*), its convexity being toward the lungs. With the exception of

FIG. 224.

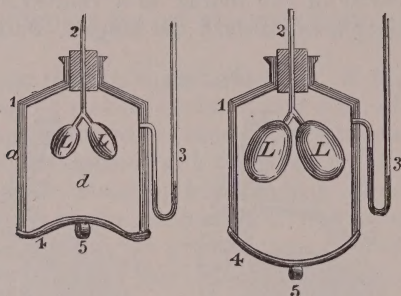


Diagrammatic sections of the body in inspiration and expiration. *A*. Inspiration. *B*. Expiration. *Tr.* Trachea. *St.* Sternum. *D.* Diaphragm. *Ab.* Abdominal walls. The shading roughly indicates the stationary air.

the central tendinous portion, the diaphragm consists of muscular fibres of the voluntary character. It presents several openings through which pass the œsophagus, aorta, vena cava, etc., and it is supplied by the phrenic nerve. During the state of repose, as we have just seen, the diaphragm presents the form of a dome or of a vaulted, arched or curved surface. If the diaphragm, however, be observed during contraction, as can be readily done by opening largely the abdominal cavity of a completely insensible living mammal, a cat, dog, or rabbit, for example, it will then be seen that through the contraction of its muscular fibres the curved surface of the diaphragm assumes more the form of a plane (Fig. 224, *A*), and that the floor of the thorax descends. The effect of the descent of the diaphragm, therefore, is to enlarge in a vertical direction the capacity of the thorax, and to rarefy the air within it. The external air being then denser than that within the thorax rushes into the latter and proportionally distends the lungs in consequence. The diaphragm through its contraction acts then as an inspiratory muscle; it need hardly be added, however, that it is

not the diaphragm, but the air, that actually distends the lungs. We are in the habit of illustrating the action of the diaphragm in respiration by the simple apparatus represented in Fig. 225. This consists

FIG. 225.



Diagrammatic view of apparatus to show the action of the diaphragm.

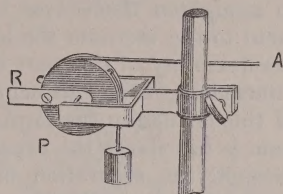
of a bell jar (*a*), the walls of which correspond to the thorax, and in which are suspended the lungs (*LL*), the trachea passing through the air-tight fitting cork. The bottom of the jar is closed in air-tight, with India rubber corresponding to the diaphragm. It is needless to say that there is no such amount of space as (*d*) corresponding to the pleural cavity in the human being in a state of health. Such being the disposition of the parts, by pulling down the India rubber (5) the air within the jar, and therefore within the lungs, becomes rarefied as indicated by the rise of the mercury within the limb (3) of the manometer. The external air will therefore rush through the trachea into the lungs, and consequently distend them. With the elevation of the India rubber the condition of the pressure of the air within and without the jar being reversed, the air will pass out of the lungs, the latter collapsing. It will be observed that the flattening of the diaphragm just referred to is most marked at its lateral portions, or the parts under the lungs, as might be expected, that part of it immediately under the heart undergoing but little change in form. As the diaphragm descends it pushes downward and forward the abdominal viscera, and as the anterior and lateral walls of the abdomen are extensible, they give way to the pressure so exerted and are protruded. With each inspiration, therefore, the descent of the diaphragm in man becomes perfectly evident through the movement of the abdomen. The action of the diaphragm in producing inspiration may be readily imitated in man and mammal just dead, by opening the abdomen and pulling the central tendon downward. The external air will rush into the lungs, and often with a distinctly audible sound. By passing a long and slender needle through the ensiform cartilage of the sternum of a completely chloralized animal, a rabbit, for example, and connecting the eye of the needle by a silk thread (Fig. 226, A), with a little boxwood pulley (P), whose movements are inscribed by the horizontal lever (R) on the recording surface, we can obtain a graphic representa-



tion of the descent and ascent of the diaphragm during respiration. Too much importance must not, however, be attached to this method of studying the movements of the diaphragm. While the vertical diameter of the chest is enlarged through the descent of the diaphragm, nevertheless, through its attachment to the sternum and false ribs during its contraction through the pulling of the sternum and the upper false ribs downward and inward, and the lower ribs upward and inward toward the vertebral column, there would be a tendency to diminish, to some extent, the capacity of the thorax. This effect is, however, counteracted by the ribs being elevated at the same time as the diaphragm descends, and through the action of certain muscles, to be described later. The elevation of the ribs is such a constant accompaniment of the descent of the diaphragm that in general terms it may be stated that inspiration is effected by the descent of the one, and the ascent of the other, and this is true, even though the breathing appear entirely diaphragmatic.

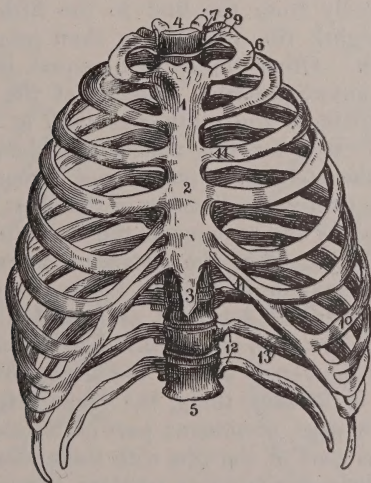
The ribs (Fig. 227) pass from their articulations with the dorsal vertebræ downward and forward; they are somewhat twisted in shape and

FIG. 226.



Boxwood pulley for recording the movements of a needle inserted in the diaphragm. A light lever is attached to the horizontal arm. (SANDERSON.)

FIG. 227.



Front view of the thorax. 1, 2, 3. The three pieces of the sternum. 4, 5. The dorsal vertebræ. 6. The first true rib. 7. Its head. 8. Neck. 9. Tubercle. 10. The seventh true rib. 11. Costal cartilages. 12. The floating ribs. 13. Groove for the intercostal bloodvessels. (LEIDY.)

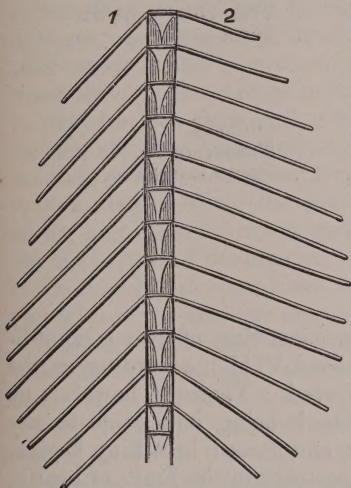
are twelve in number. The upper seven or true ribs are articulated with the sternum, of the remaining five or false ribs, the eighth, ninth, and tenth are joined to the seventh rib, the last two ribs, viz., the

eleventh and twelfth, are unattached anteriorly and are hence known as floating ribs. As the ribs are elevated they recede from each other, the distance between them being increased; they are at the same time rotated outward, assuming a more horizontal position, and in tending to straighten themselves become less curved. Through their attachment to the sternum the lower portion of the latter is thrown forward, the flexibility of this part of the thorax being mainly due to the sternal attachment of the ribs being cartilaginous and not osseous. The effect of this change in the form, position, and direction of the ribs and sternum is to enlarge the capacity of the chest in every direction vertically through the separation of the ribs, laterally through their rotation outward and straightening, antero-posteriorly, through the movement forward of the sternum. As the air rushes in, distending the lungs of the expanding chest, it is evident, therefore, that inspiration is produced through the elevation of the ribs as well as through the descent of the diaphragm. The extent of the increase of the capacity of the chest through the elevation of the ribs is greatly influenced by the length, degree of curvature, character of the angles of the ribs, etc. Thus from the ribs being directed obliquely downward and forward when elevated, and assuming a more horizontal position their external ends recede from the posterior wall of the thorax and increase proportionally its antero-posterior diameter. As the ribs are elevated they remain nearly parallel to each other, it follows, therefore, that the inspiratory effect produced by this movement of the ribs will be proportional to the length, or, more accurately speaking, to the length of the chord of the arc represented by the curve of the rib. The length, however, varies considerably, increasing rapidly from the first to the fifth rib, attaining its maximum at the eighth rib, diminishing then progressively from the ninth to the twelfth. Other things being equal, it follows, then, that the increase in the antero-posterior diameter of the chest is greater at the level of the seventh to the ninth ribs than at the upper or lower part of the thorax. It is for this reason that during inspiration the inferior portion of the sternum moves so much more forward than the upper portion. The transverse diameter of the chest, on the other hand, is greatly influenced by the amount of the curvature of the ribs, and this varies considerably. Thus the curvature increases from the first to the third ribs, the maximum amount being about that of the sixth; there is but little difference, however, as regards the curvature of the ribs included between the sixth and ninth. The amount of the curvature can be measured by the versed sine of the arc of the circle represented by the rib, or, what is the same thing, the distance from the middle line of the thorax to the most prominent part of it laterally. The angle made by the osseous part of the ribs with their sternal or costal ones, and the length of their cartilaginous portions increase from the fourth to the seventh. Consequently it is in this part of the thorax that the increase of capacity due to the elasticity and flexibility of the cartilage is greatest. The different extent to which the capacity of the thorax is enlarged in its various diameters during inspiration, the influence due to the variation in the length, curvature of the ribs, etc., are shown by the diagrams (Figs. 228, 229, 230, and 231) illustrating the admirable



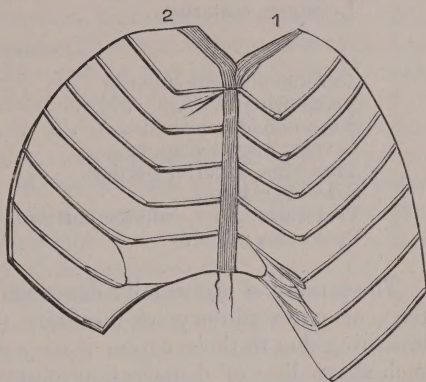
and exhaustive work of Sibson.<sup>1</sup> Let us consider now the muscles which elevate the ribs, and so, together with the action of the diaphragm, cause inspiration.

FIG. 228.



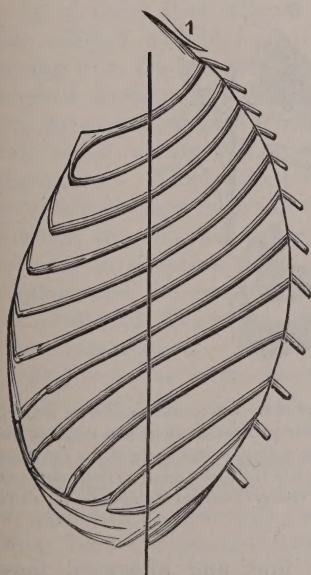
Dorsal region.  
Expiration.      Inspiration.

FIG. 229.



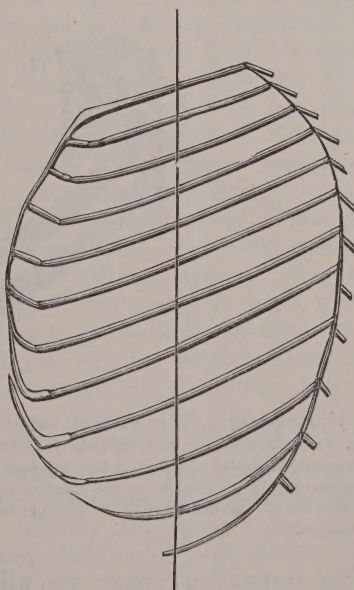
Anterior region of the thorax.  
Inspiration.      Expiration.

FIG. 230.



Expiration.

FIG. 231.



Inspiration.

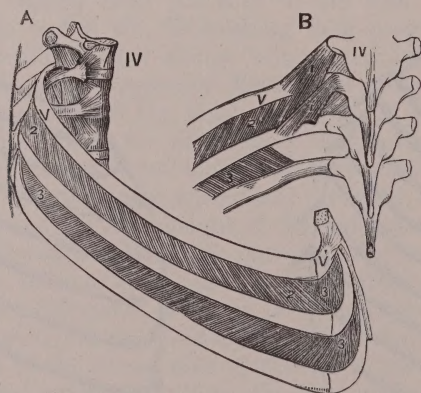
<sup>1</sup> Phil. Trans., 1846.

TABLE LVIII.—MUSCLES OF RESPIRATION.

| Inspiration.                                 |  | Expiration.            |  |
|----------------------------------------------|--|------------------------|--|
| Ordinary.                                    |  |                        |  |
| Diaphragm . . . . .                          |  | Internal intercostals, |  |
|                                              |  | osseous portion.       |  |
| External intercostals.                       |  |                        |  |
| Internal intercostals, sternal portion . . . |  | Triangularis sterni.   |  |
| Scaleni . . . . .                            |  | Infra costales.        |  |
| Levatores costarum.                          |  |                        |  |
| Auxiliary.                                   |  |                        |  |
| Serratus posticus superior . . . . .         |  | Oblique.               |  |
| Accessorius . . . . .                        |  | Transversalis.         |  |
| Sterno-cleido-mastoid . . . . .              |  | Sacro Lumbalis.        |  |
| Levator anguli scapulæ.                      |  |                        |  |
| Trapezius, superior portion.                 |  |                        |  |
| Serratus magnus.                             |  |                        |  |
| Pectorales major, inferior portion.          |  |                        |  |
| Pectorales minor.                            |  |                        |  |

These muscles are usually described as consisting of two sets, ordinary or extraordinary, or auxiliary (Table LVIII.), according as the breathing due to their action is easy or forced. There is, however, no such sharp line of demarcation observable, it being impossible to say just where ordinary easy breathing ends, and forced breathing begins, great difference being observed in this respect within the limits of health, according to individual peculiarities. There are certain muscles, however, such as the external intercostals, scaleni, etc., which intervene in

Fig. 232.



View of several of the middle dorsal vertebrae and ribs, to show the intercostal muscles (A. B.).  $\frac{1}{3}$ . A. From the side. B. From behind. 1, 1. The levatores costarum muscles, short and long. 2. The external intercostal muscles. 3 The internal intercostal layer shown, in the lower of the two spaces represented, by the removal of the external layer, as seen in A in the upper space, in front of the external layer. The deficiency of the internal layer toward the vertebral column is shown in B. (After CLOQUET.)

easy inspiration; these we will consider first, and afterward those coming into play when the breathing is exaggerated. That the external intercostal muscles (Fig. 232) are inspiratory in function one would



infer from their attachments, and the direction of their fibres. Passing from rib to rib from above downward, and from behind forward, in contracting these muscles, will approximate and elevate the ribs. Experiment justifies this view of the inspiratory function of the external intercostal muscles, since, if they be exposed in a living animal with each inspiration, they will be seen in contracting to elevate the ribs. Inasmuch, however, as the general direction of the sternal portion of the internal intercostals is also from above downward, and rather forward than backward, through the change in the curve of the rib, analogy would lead us to suppose that their action is the same as that of the external intercostals, and that they must, therefore, be also regarded as inspiratory in function. This view is confirmed by the observations of Bernard,<sup>1</sup> made upon a man in whom the pectoral muscle was so atrophied as to permit of an experimental investigation of the function of the partly exposed sternal portion of the internal intercostal muscle. When the sternal part of the muscle was stimulated, the cartilage of the second rib was elevated, and with it the anterior extremity of the corresponding osseous rib.

The scaleni passing obliquely downward from their origin, the transverse processes of the lower six cervical vertebræ, to their insertion, the first and second ribs, in acting from their origin during contraction will elevate these ribs, and indirectly the whole thorax. To prove that the scaleni do act in this way it is only necessary to squeeze between the fingers the part of the neck including these muscles to feel them contract with each inspiration. The movement then experienced, the so-called respiratory pulse of Magendie,<sup>2</sup> becomes very evident when the superior part of the chest is much dilated. The action of the scaleni is not only to elevate the ribs, but to fix the first rib as an origin from which the intercostal muscles that elevate the ribs can act. Ordinary inspiration is also effected by the levatores costarum (Fig. 232), as these muscles, arising from the transverse processes of the twelve dorsal vertebræ, and inserted fan-like into the upper edges of the ribs between the tubercles and the angles in contracting, elevate the ribs. The action of the muscles, which we have just considered, usually suffices to produce easy inspiration. When breathing, however, becomes difficult, labored, or very difficult, then inspiration is aided through the contraction of several muscles, the serratus posticus superior, accessorius, sterno-cleido-mastoid, levator anguli scapulæ, superior portion of the trapezius, serratus magnus, and the pectoral muscles. It is not necessary to dwell upon the anatomical disposition of these muscles to prove their importance in labored inspiration. It is evident that the serratus posticus superior passing from the vertebral column to be inserted into the second, third, fourth, and fifth ribs, will, in contracting, elevate the ribs, that the accessorius, extending from the last cervical vertebræ to the angle of the ribs, will produce the same effect. The sterno-cleido-mastoid acts upon the clavicle and sternum, and the levator anguli scapulæ, trapezius, and serratus magnus, through the scapula. Finally, the upper extremities being fixed, the pectoral muscles reversing their action, will elevate the

<sup>1</sup> Physiologie, tome iii. p. 269.

<sup>2</sup> Précis élémentaire de physiologie, 2d ed., tome ii. p. 323.

ribs; their force, under such circumstances, acting upon the thorax, instead of from it.

### EXPIRATION.

Expiration is essentially a passive process, consisting in the return of the thorax to the condition in which it was before inspiration. The ascent of the diaphragm, and the descent of the ribs in diminishing the capacity of the thorax, cause the expulsion of the air, or expiration. The relaxation of the inspiratory muscles is, however, accompanied by the contraction of certain muscles which together with the elasticity of the lungs aids in expelling the air from the chest. Inasmuch as the fibres of the osseous portion of the internal intercostal muscles (Fig. 232) pass from rib to rib in exactly the opposite direction as those of the internal intercostal—that is, from above downward, but backward—we would naturally conclude that in contracting they would depress the ribs instead of elevating them, that their function is expiratory instead of inspiratory. Experiment proves that this view is correct, since, if the osseous portion of the internal intercostal muscles be exposed in a living animal by dissecting off the external ones, they will be found to contract during expiration. We generally illustrate this antagonism in the action of the internal and external intercostal muscles by a simple mechanical arrangement known as Hamberger's apparatus, though it was really invented by Bernouilli. This consists (Fig. 233, *A*) of two bars (*a* and *b*), which are attached

FIG. 233.

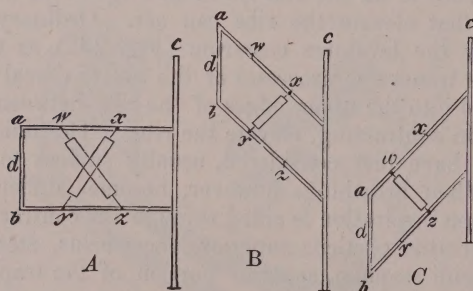


Diagram of models illustrating the action of the external and internal intercostal muscles.  
B, inspiratory elevation; C, expiratory depression. (HUXLEY.)

on the one hand to a long vertical rod (*c*) firmly supported, and, on the other hand, to a short one (*d*). The two bars, the long and the short vertical rods, represent respectively the spinal column, two ribs, and a portion of the sternum. The two bars (*a* and *b*) are maintained in the horizontal position by two elastic bands (*wz* and *xy*), which are so attached that as they pass from bar to bar they cross each other at right angles. The elastic band (*xy*) passing from above, downward and forward, represents the external intercostal muscle, the band (*wz*) passing from above downward, but backward, the osseous portion of the internal intercostal muscle. If the band (*wz*) be removed (Fig.



233, B), there being nothing to oppose the elasticity of the band  $xy$ , or the external intercostal muscle, the bars or ribs will be elevated. If the band  $wz$  be now replaced, and the band  $xy$  removed (Fig. 233, C), then the bars or the ribs will be depressed, there being nothing to oppose the elasticity of the band  $wz$ . While the action of the external and internal intercostal muscles in respiration, as we have described them, appears to be capable of demonstration in the living animal and imitated by mechanical contrivances, nevertheless, it must be admitted that the action of these muscles has given rise to more discussion than that of all the other muscles in the body, and that the most diverse opinions have been offered, and are still held as to their function. Thus, while according to Borelli, Haller, and Cuvier, both the external and internal intercostal muscles are inspiratory, just the opposite opinion, that they are both expiratory, was held by Vesalius, Beau and Maissiat and Galen. Bartholinus considered the external intercostals to be expiratory, the internal inspiratory, while Spigelius and Vesling held the external intercostals to be inspiratory, the internal expiratory. The external and internal intercostals were regarded at once inspiratory and expiratory by Mayow and Magendie, while according to Arantius and Cruveilhier, both the internal and external intercostals are passive in inspiration and expiration, performing simply the office of a resisting wall in respiration.

Whatever view may be held as to the function of the internal intercostal muscles in respiration, there can be no doubt that the triangularis sterni and infracostalis, and usually the serratus posticus inferior are expiratory muscles. The triangularis sterni acting from its origin, the ensiform cartilage, the lower border of the sternum, and the lower costal cartilages, in drawing down the cartilages of the second, third, fourth, and fifth ribs must diminish the capacity of the chest. The infracostales produce the same effect, their fibres passing from the inner surface of one rib to the inner surface of the first, second, and third below, their action being from below upward. The muscles that we have just described usually suffice in tranquil expiration; in difficult or labored expiration, in the acts of blowing, phonation, etc., the muscles entering into the formation of the abdominal walls also come into play. The general effect of these muscles, viz., the external and internal, oblique transversalis, sacro-lumbalis, etc., is in contracting to push up the abdominal viscera and diaphragm into the thorax, diminishing its capacity in the vertical diameter; these muscles, however, in being attached to the ribs or costal cartilages depress at the same time the ribs and consequently diminish the thorax in its antero-posterior and transverse diameters also. The effect of the action of these muscles is, therefore, to aid powerfully in the expulsion of the air from the chest in forced expiration. As their action and that of the diaphragm is more or less voluntary, and being at the same time opposed to each other, the intensity and duration of expiration can, to a great extent, be regulated arbitrarily; the importance of this relation is well seen in singing, in performing upon wind instruments, etc., the skill exhibited depending largely upon the nicety with which the contractions of these muscles can be adjusted to each other.

We have already seen that the lungs are elastic, and were it not for the pressure exerted upon the inner surface of the lungs by the inspired air the lungs would collapse in virtue of this elasticity, and a considerable space in consequence would be left between the lungs and the chest-wall. The natural tendency of the lungs to contract through their elasticity is well seen when air is allowed to enter the pleural cavities. Under such circumstances the atmospheric pressure being exerted equally on both the inner and outer surfaces of the lungs, there is nothing to oppose their elasticity and the lungs therefore collapse. If one end of a tube be passed into the trachea of an animal just dead, and ligated, and the other end be inserted into a water or mercurial manometer, with the entry of air through an opening made into the pleural cavity the lungs will collapse in virtue of their elasticity, the level of the liquid in the proximal end of the manometer will be observed to fall, that of the distal end to rise, the difference in the level of the two indicating and measuring the amount of elastic force exerted. It was in this way that Carson<sup>1</sup> first showed that the elasticity of the lungs in the calf, sheep, or dog would support a column of water twelve to eighteen inches in height, and in the rabbit six to ten inches. The elastic force of the lungs amounting to half a pound on the square inch in man, not only aids the expiratory muscles, therefore, in expelling the air from the chest, but through the suction force exerted also elevates the diaphragm, restoring it to the dome-like form it presents before inspiration. Finally, the contractility of the bronchi and elasticity of the thoracic walls themselves contribute in expelling the air from the chest. It is usually considered that in inspiration the upper ribs are elevated before the lower, and in expiration the lower ribs are depressed before the upper, the motion being wave-like from above downward and from below upward. According to the recent observations of Rausome<sup>2</sup> it would appear, however, that the reverse obtains, the lower ribs in inspiration being elevated first and the upper ones last, and that in expiration it is the upper ribs that are depressed first and the lower ones last. Even if such is the case, it is not inconsistent with the view that the upper part of the chest is moved first in inspiration, the lowest last, since if the scaleni act before the intercostal muscles the upper ribs would be elevated before the lower by the action of the scaleni, even if the lower intercostal muscles contracted before the upper. It is possible that the difference of opinion in reference to the order in which the ribs are elevated and depressed is due to the action of the intercostal muscles, being considered without reference to the simultaneous action of the other respiratory muscles.

While, in a general way, it can be said that inspiration is due to the descent of the diaphragm and the ascent of the ribs, and expiration to the ascent of the diaphragm and descent of the ribs, nevertheless there is a noticeable difference, more particularly studied by Bean and Maissiat,<sup>3</sup> as to the relative importance of the parts played by the diaphragm and the ribs, as observed in the breathing of the two sexes. Thus while in the male sex breathing is accomplished by the diaphragm and the in-

<sup>1</sup> Phil. Trans., 1820.

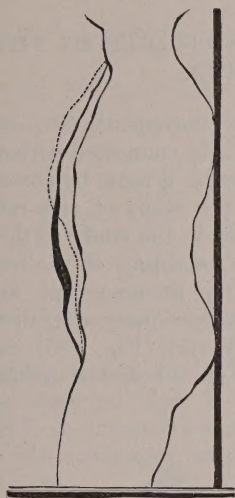
<sup>2</sup> Stethometer, 1876, p. 37.

<sup>3</sup> Archives générales de médecine, 1843, 3d ser. t. xv. p. 397; 4th ser. 1843, t. i. p. 265; t. ii. p. 257; t. iii. p. 249.



ferior part of the thorax, or the portion below the sixth rib, in the female sex it is the superior part of the chest, or that above the seventh rib (Figs. 234, 235), which takes an active part in respiration. It might be

FIG. 234.



The changes of the thoracic and abdominal walls of the male during respiration.

FIG. 235.



The same in the female. (HUTCHINSON.)

supposed that the superior costal type of breathing characteristic of the female is due to peculiarities of dress, such as the wearing of corsets, the squeezing of the waist, etc., which would interfere with or prevent even the lower part of the chest expanding. That this is not the only cause, however, is proved by the fact that the superior costal type of breathing prevails even in females that have never at any time worn any kind of clothing whatever. That the superior costal type of breathing is of advantage to the female is obvious when one considers the extent to which the abdominal viscera and diaphragm are pushed up, as is the case during pregnancy, through the enlargement of the uterus. Under such circumstances, if the breathing of the female was of the inferior costal type and diaphragmatic, like that of the male, inspiration would be difficult and labored. It is also on account of this peculiarity in breathing that women can tolerate with so little inconvenience large accumulations of fluid in the abdominal cavity. While in the adult the diaphragmatic inferior costal type of respiration of the male as contrasted with the superior costal type of the female is perfectly evident, the distinction in young children is not noticeable. Indeed, children under about ten years of age breathe almost entirely by the diaphragm. It is not, as a general rule, until near puberty that the distinction in breathing characteristic of the adult sexes becomes apparent. Haller,<sup>1</sup> however, states that the difference in the types of breathing in the sexes in some cases manifested itself as early as the first year.

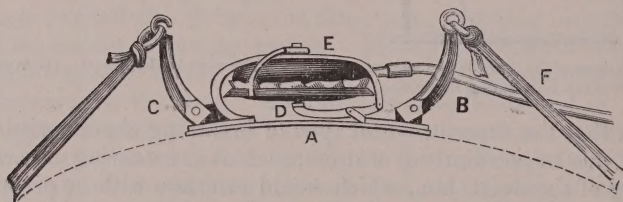
<sup>1</sup> *Prælectiones Academiæ*, tomus v. p. 144.

## CHAPTER XXVIII.

### RESPIRATORY MOVEMENTS AS STUDIED BY THE GRAPHIC METHOD.

NOTWITHSTANDING that the respiratory movements are evident to the eye, and that the respiratory organs can be connected without injury with apparatus for recording their movements, it must be admitted that the application of the graphic method to the study of respiration does not give as satisfactory results as is the case in the study of the circulation. Of the instruments devised for the recording of the respiratory movements graphically, we have found the pneumograph and stethometer to be among the most useful. The pneumograph, invented by Marey,<sup>1</sup> in its present form, modified by Verdin (Fig. 236), consists of an elastic plate A, having an area of 26 cm. (4 square inches), which

FIG. 236.



Pneumograph.

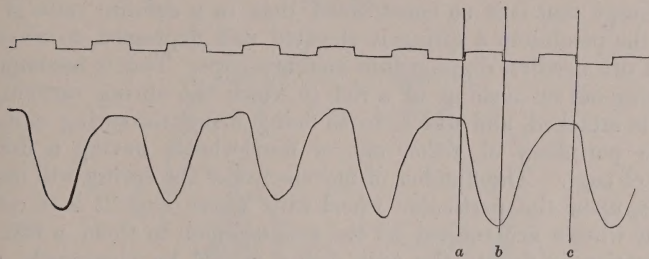
is applied to that part of the chest whose movements it is desired to study, and firmly secured there by tapes passing around the neck from the edge of the plate and around the chest from the pillars B and C, projecting from the plate. To the lower end of the pillar B is attached a spring (D), the free end of which is so attached that it presses against the elastic membrane covering in the lower surface of an air-drum (E), the latter communicating through a caoutchouc tube (F), with a recording tambour. With the bending of the elastic plate A through the expansion of the chest, the pillars B and C recede from each other, the spring D ceasing at the same time to press on the membrane of the air-drum E. The air within the drum being therefore rarefied, the air from the recording tambour is drawn into it, and the lever attached to the tambour is depressed. With the contraction of the chest the elastic plate straightens, the pillars approach each other, the spring presses again the elastic membrane, the air is driven out of the drum into the tambour, and the lever is elevated. The depression of lever corresponds, therefore, to inspiration, the elevation to expiration. By placing the lever of the recording tambour in contact with the blackened surface of

<sup>1</sup> La methode Graphique, p. 542



the cylinder moving by clockwork, we obtain a trace like that of Fig. 237, representing the breathing of a man æt. thirty years. In this trace the distance from *a* to *c* represents one inspiration; the part of the trace from *a* to *b*, due to the descent of the lever, being inspira-

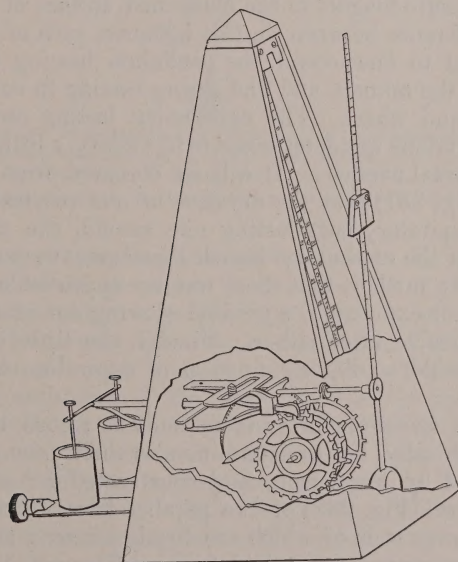
FIG. 237.



Upper line, trace of chronograph. Lower line, trace of respiratory movements. Taken with pneumograph.

tory in origin, that of *b* to *c* due to the ascent of the lever expiratory. It will be observed that the inspiratory movement, as recorded in its trace, *a* to *b*, is extremely abrupt, becoming more gradual at its close, and that the expiratory movement (*b* to *c*) is equally abrupt at the

FIG. 238.



Metronome.

beginning, but that the gradual movement at the termination is more marked even than in the case of the inspiratory movement. In order to determine accurately the number of respirations in a given time, the length of time of one respiration, the relative duration of one expira-

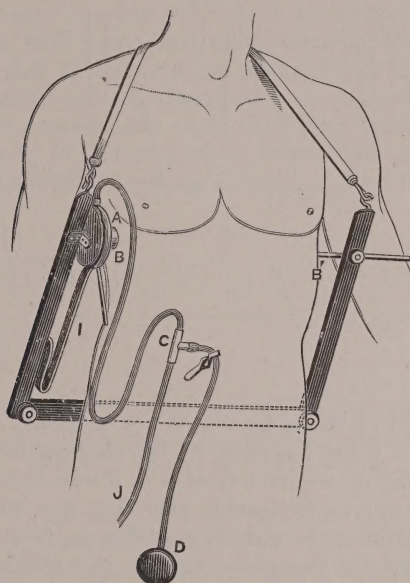
tion and inspiration; the existence of pauses, if any, after inspiration and expiration, it is necessary to make use of some chronographic apparatus, by means of which we can record graphically the time elapsing during which the respiratory movements are being studied. For this purpose we make use of the metronome in connection with an electro-magnet. The metronome (Fig 238) is the same as that used by musicians, except that it is so constructed that, in a definite ratio of each beat of the pendulum a spring is elevated and depressed, to which are attached two needles, dipping into mercury cups. This is accomplished by drawing out or pushing in a rod to which the spring carrying the needles is attached, and which, by so doing, brings the spring in contact with the periphery of either one or four wheels having a different number of cogs. The number of movements of the spring will depend, therefore, upon the particular wheel with whose cogs it is in contact. The four wheels are rotated by the axis common to them, a fifth one, whose motion is due to the axis, being moved by clockwork, which is regulated by a pendulum. With the elevation of the spring the needles are raised out of the mercury in the cups, and with its depression they sink into it again. As the needles are elevated and depressed the current, passing from the battery through the needles and mercury to the electro-magnet, is made or broken, and the marker connected with the latter synchronously depressed and elevated in the manner already described. In the trace obtained by applying the marker of the electro-magnet to the blackened surface of the revolving cylinder, the difference between, in this instance, each of the two vertical lines is equal to one second, the pendulum beating at the rate of sixty seconds to the minute, and the spring coming in contact with the cogs of the second wheel. The experiment lasting one minute, the number of respirations was determined to be twenty, a little over what we shall see is the usual average. It will be observed from a comparison of the traces (Fig. 237) that the duration of one respiration was three seconds, the inspiratory part lasting one second, the expiratory two seconds, and that the expiratory lasted, therefore, twice as long as the inspiratory effort; further, that there was no appreciable pause, either after inspiration or expiration, a gradual slowing up of the movement only being noticeable after either. Finally, the little undulations of the trace noticeable at the termination of expiration are cardiac in origin.

The object of the stethometer is not only to record the respiratory movements graphically, but to determine also their extent. The instrument, as devised by Sanderson, and constructed for the author by Hawksley, consists (Fig. 239) of two parallel bars, 30 cm. (12 inches) in length, the lower ends of which are firmly screwed at right angles into a crossbar so as to form a rigid frame. Through one of the bars passes a slender rod (B'), terminating in a convex ivory knob (B). By means of a screw the extent to which the rod and knob are pushed within the frame can be varied as needed and firmly fixed. The opposite bar carries a spring (I), the upper part of which carries a horizontal pin, terminating at one end in an ivory knob, and at the other in a brass disk, the latter being in contact with the tambour (A) attached to the



upper part of the bar. The two ivory knobs not only face each other, but lie in the same axis. The receiving tambour communicates by means of the tube J with the recording portion of the apparatus, and also through the T tube with an India-rubber ball, the latter being used to fill both tambours and communicating tube (D).

FIG. 239.

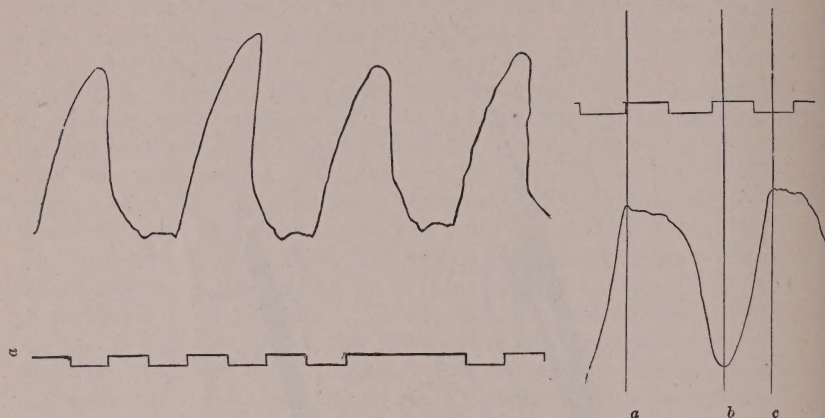


Recording stethometer. A. Tympanum. B. Ivory knob. B'. Rod which carries the knob opposed to B. C, T-tube, by which A communicates, on the one hand, with the recording tympanum, on the other with an elastic bag (D). The purpose of the bag is to enable the observer to vary the quantity of air in the cavity of the tympana at will. The tube leading to it is closed by a clip when the instrument is in use. (SANDERSON.)

The manner of adapting the stethometer to the chest will depend upon the part whose movement it is desired to examine. If, for example, we wish to obtain a graphic representation of the movements of the chest in a transverse direction, let the instrument be so applied that the ivory knobs will press upon the eighth rib. The knob being firmly fixed with the expansion of the chest, the rib will press outwardly the knob of the receiving tambour, the air will be driven out of it into the recording one, and the lever will be elevated; with the contraction of the chest the air will return from the recording to the receiving tambour lever, and the lever will be depressed. With the stethometer, therefore, inspiration corresponds to the elevation of, and expiration to, the pressure of the recording lever, just the opposite to what happens, as we have seen, when the pneumograph is used. To obtain a trace representing the enlargement of the chest in an antero-posterior direction, the stethometer can be applied so that the ivory knobs are in contact with the manubrium sterni and the third dorsal spine, or the ensiform cartilage and the tenth dorsal spine respectively. Fig. 240 is that of the trace obtained by the stethometer as applied to the seventh ribs

in the case of a healthy man, æt thirty years, and is a graphic representation, therefore, of the respiratory movements, in so far as they depend upon the enlargement of the chest in a transverse direction in

FIG. 240.



that particular part of the chest. It is not necessary to dwell upon the peculiarities of the trace recorded by the stethometer. It will be observed that the part of the trace from *a* to *b* corresponds to the inspiration, that from *b* to *c* to expiration, and that the relative duration of inspiration to expiration is somewhat different from that observed in the trace obtained by the pneumograph, the number of respirations being in this case eighteen to the minute. Here and there, it will be noticed that the breathing became more marked. In order to determine the extent of the enlargement of the chest by the stethometer, the instrument must be graduated. This can be done either by placing successively between the ivory buttons rods differing by a known length, and observing the different levels to which the lever is elevated, according to the rod used, the vertical distances between the horizontal lines made by the lever corresponding to a definite increase in the distance between the ivory knobs of the particular diameter of the chest examined, or by placing directly underneath the ivory knobs a graduated rod, carrying a vertical slide, which can be pushed against the movable knob, and noticing the different heights to which the recording lever is elevated. In the trace represented in Fig. 240, the elevation of the lever through the space *a* to *b* corresponds to an increase of about 2 mm. ( $\frac{1}{2}$ th of an inch) in the lateral diameter of the chest.

While in tranquil breathing the increase in the antero-posterior diameter of the thorax may be only one mm. ( $\frac{1}{25}$ th of an inch) inforced breathing, according to Rausome,<sup>1</sup> it may amount to as much as 12 to 30 mm. ( $\frac{1}{2}$  to 1.2 in.).

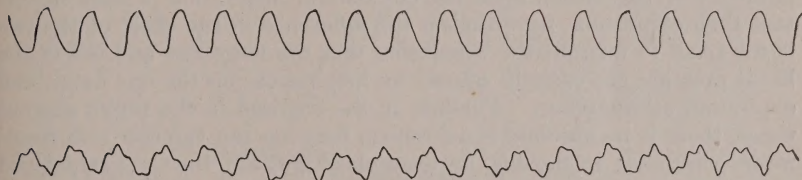
In describing the circulation it will be remembered that attention was called to the large undulations present in the curve of blood pressure,

<sup>1</sup> Sanderson : Handbook Phys. Lab., p. 302.



and which at that time were simply stated as being, to a certain extent at least, respiratory in origin. In order to study the influence of the respiration upon the circulation, it is essential that a comparison should be made between the curves of blood pressure and respiration taken simultaneously. In the case of man this can be done by applying at the same time the cardiograph and pneumograph and comparing the traces so obtained, or in an animal by connecting a recording tambour with its trachea, and comparing the respiratory trace so obtained with that of the pressure of the blood in its carotid artery, taken in the manner already described. A comparison of the traces of the respiratory movements and the blood pressure in a rabbit (Fig. 241), taken by the latter method, shows that in this case at least the inspiration is almost, if not absolutely, synchronous with the rise of

FIG. 241.

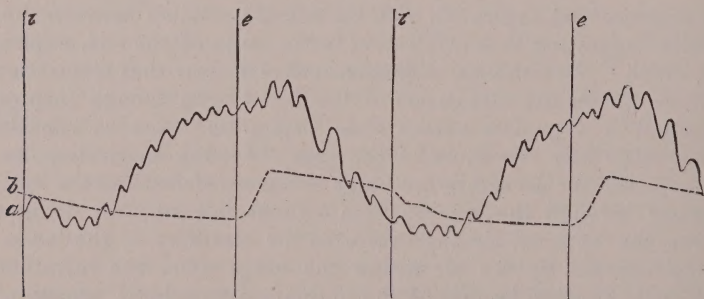


Traces of blood pressure and respiratory movements of rabbit taken simultaneously. Upper trace blood pressure. Lower trace respiratory movements.

blood pressure and expiration with the fall, the relation between the two naturally suggesting that inspiration is the cause of the one, expiration of the other. Nevertheless, reflection makes it clear that respiration on the whole favors the circulation of the blood even though inspiration promotes it to a greater extent than expiration. Let us consider in detail a little why this must be the case. During inspiration, as the chest expands, the air within the lungs becomes rarefied and the external air passes through the trachea from without inward. In doing this, however, the external air has overcome the elasticity of the lungs, the pressure exerted by the air within the lungs upon the intrathoracic vessels will therefore be that of the ordinary atmospheric pressure, less the pressure due to the elasticity of the lungs. Suppose, for example, that the pressure exerted by the elasticity be half a pound to the square inch, then the pressure exerted by the air within the lungs upon the great bloodvessels will be only fourteen and a half pounds, that of the atmosphere being fifteen pounds. The effect of this difference of the atmospheric pressure within and without the chest during inspiration is that a greater quantity of venous blood being forced through the great veins toward the right auricle of the heart and thence through the lungs, a proportionately greater quantity of arterial blood passes, therefore, through the left ventricle into the aorta, the result of which will be to increase the blood pressure. The flow of the venous blood from the periphery to the heart being promoted by inspiration, it might be supposed that the flow of the arterial blood in the reverse direction would be proportionally retarded. It must be remembered, however, that the pressure exerted by the extrathoracic air upon the thin, flaccid

walls of the veins will produce a greater effect than upon the thick, resisting coats of the arteries, and that the pressure of the external air so exerted is not much in excess of the resistance that the heart has to overcome in driving the blood from the ventricle into the arterial system during its systole. Further, during expiration the conditions are the reverse of those obtaining in inspiration, the intrathoracic pressure being now greater than the extrathoracic. The pressure so exerted now adds itself to the elasticity of the arteries and promotes the flow of the blood from the heart to the periphery, while the valves prevent to any extent regurgitation of the venous blood. Respiration, on the whole, therefore, favors the circulation, since inspiration aids the flow of the venous blood without offering any great obstacle to the arterial flow, while expiration favors the flow of the arterial blood without retarding to any extent the venous flow, and while it is true that in the influence of respiration upon the circulation, inspiration is more important than expiration, nevertheless the difference in the effect of the two is too small to warrant the conclusion that the large rise and fall in the blood pressure are entirely caused by inspiration, on the one hand, and expiration on the other. Further, in the dog and in the rabbit also, at times, there is no absolute synchronism between the vascular and respiratory rhythms; in the dog, for example (Fig. 242), the rise in the blood pressure lasting not only to the end of the inspiration, but during a part

FIG. 242.



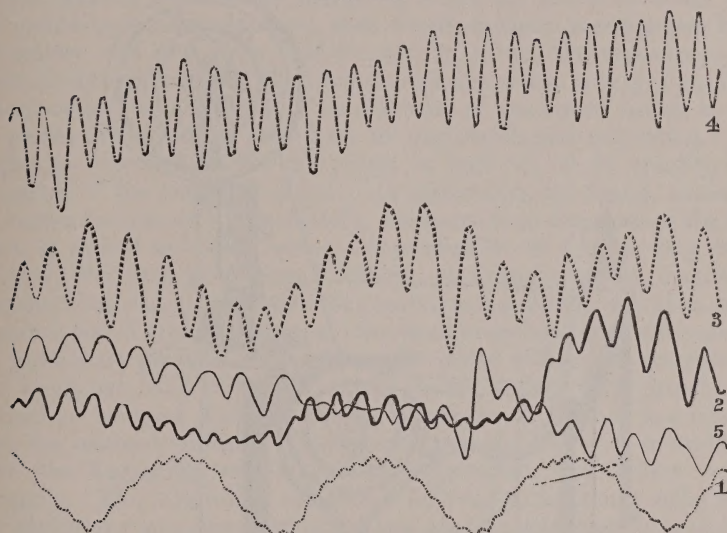
Comparison of blood pressure curve with curve of intrathoracic pressure. To be read from left to right. *a* is the blood-pressure curve, with its respiratory undulations, the slower beats on the descent being very marked. *b* is the curve of intrathoracic pressure obtained by connecting one limb of a manometer with the pleural cavity. Inspiration begins at *i*, expiration at *e*. The intrathoracic pressure rises very rapidly after the cessation of the inspiratory effort, and then slowly falls as the air issues from the chest; at the beginning of the inspiratory effort the fall becomes more rapid. (FOSTER.)

of expiration, and the fall in blood pressure lasting not only till the end of expiration, but during a part of inspiration. This want of synchronism between the rhythms, together with the fact that the large undulations characteristic of blood pressure persist even after all respiratory movements have ceased, proves that there must be some influence other than respiration concerned in their production. Thus if an animal, a rabbit, for example, be curarized, in which condition the respiratory nerves cease to act altogether, the heart continues to beat, artificial respiration be maintained and a trace of the blood pressure be taken, a curve like that of Fig. 242 will be obtained. If now the artificial respi-



ration be discontinued the blood pressure rises, while the character of the curve changes; nevertheless, a rhythmical rise and fall still occur, like that of Fig. 242, *b*. The curve so obtained is known as that of Traube, from having been first described by that observer. Inasmuch as respiration has entirely ceased and both vagi even being divided, it

FIG. 243.



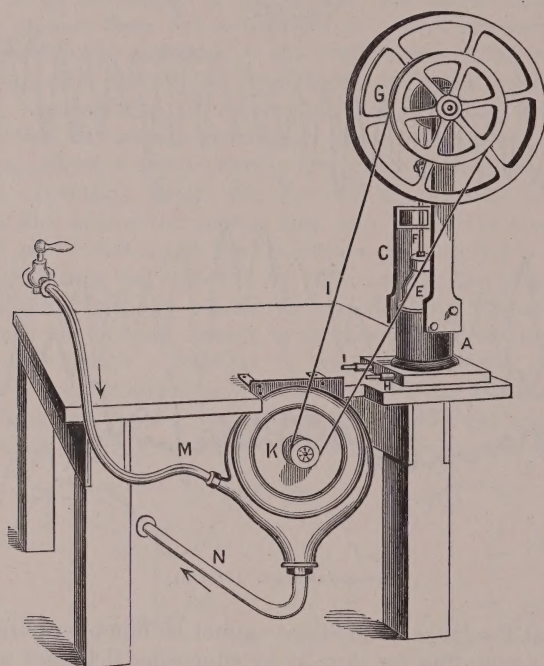
Traube's curves. (FOSTER)

is evident that the large undulations cannot be due to respiration. The only way of accounting for them is by supposing that they are of vasomotorial origin, the rhythmic rise and fall in the blood pressure, through the rhythmic constriction of the arteries, being due to a rhythmic stimulus emanating from the vasomotor centre of the medulla. This view is confirmed by the following facts: that the phenomena in question are much less marked if the spinal cord be divided below the medulla, and that the undulations persist even after the heart itself be removed, and the circulation be maintained artificially. It is difficult to understand why the vascular rhythm, due to the vasomotor centre, should simulate and be superimposed upon the respiratory rhythm due to the medullary respiratory centre, unless through conditions in the evolution of the animal and which we are not familiar with, the two centres in the medulla have been gradually brought to act synchronously. It will be seen, therefore, that while the rise and fall in the blood pressure are influenced by inspiration and expiration, the phenomenon is independent of respiration, or probably that both are influenced by a common cause, the condition of the blood in the medulla acting as a stimulant to the vascular and respiratory centres.

In the study of the circulation and respiration, as in the present case, it is often necessary to maintain artificial respiration. We take the opportunity, therefore, of describing the apparatus made for us by Hawksley,

of London, and which we have found useful in effecting this object. The apparatus is essentially a mercurial pump, and consists (Fig. 244) of two chambers, cast-iron cylinders (A and B, B not seen in Fig. 244), concentrically disposed and firmly fixed in a solid frame (C). The

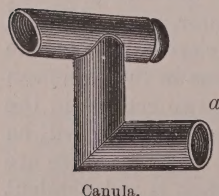
FIG. 244.



Mercurial pump for artificial respiration.

upper space D between the cylinders contains mercury, through which the bell-jar E covering the internal cylinder B is elevated or depressed by the vertical motion of the rod F connecting it with the wheel G, to the rotation of which the motion of the rod is due. The internal cylinder B opens externally through the two brass nozzles H and I. Each of these nozzles is provided with a valve, which, however, open in opposite directions—that of H from without inward, that of I from within outward. As the bell-jar is elevated the air passes through H into the internal cylinder, and as it descends the air passes out of it through I, and thence by means of a tube terminating in a

FIG. 245.



Canula.

canula to the trachea of the animal whose respiration is to be maintained artificially. The canula that we use for insertion into the trachea is that of Ludwig, and consists of a tube of glass (Fig. 245) of which the end *a*, when *in situ*, faces the lungs and through which the air to be inspired passes, the expired air escaping by a small opening



The rotation of the wheel G, to which the action of the respiratory pump is due, is effected by a Backus water motor (K) to which the wheel is connected by the band I. The water supplying the motor is conveyed to it from the hydrant in the laboratory by the tube M and away from it to the waste-pipe by the tube N.

In ordinary tranquil respiration no sound is heard unless the ear be applied directly to the chest, excepting when the mouth is closed and the breathing exclusively nasal, then a soft murmur accompanies both inspiration and expiration. If the ear, or, better, the stethoscope, be successively applied over the trachea and the chest, a very noticeable difference will be observed in the character of the sound heard, as the air passes through these parts both in inspiration and expiration. As might be expected, as the air passes in and out of the trachea, the character of the sound is tubular. In inspiration, the sound, attaining its maximum intensity immediately, maintains it to the close of the act, when it rather suddenly ceases. Immediately, or after a very brief interval, the expiratory sound follows, attaining soon its maximum intensity, but, unlike the inspiratory sound, rather dying away than ceasing abruptly. As the air passes into the small bronchial tubes and expands the pulmonary air cells it gives rise to a sound difficult of description, and which can only be appreciated by being heard. It is usually described as being of a breezy or vesicular character, and is less intense than the tracheal murmur. The sound gradually increases in intensity from the beginning to the end of inspiration, and ceases rather abruptly. The inspiratory murmur is followed without any interval by the expiratory one, lower in pitch, less intense, and lasting a shorter time. It must be mentioned, however, that the expiratory murmur is frequently absent. Certain modifications of the respiratory sounds and movements, such as snoring, coughing, sneezing, sighing, yawning, laughing, sobbing, and hiccoughing need only a passing notice, since they are simply exaggerations of either the inspiratory or expiratory movements, or of both. Snoring, a sound too familiar to need description, occurs when the mouth is open, and is due to a vibration or flapping of the velum palati between the two currents of air from the mouth and nose together with a vibration of the air itself. Coughing and sneezing, usually involuntary acts, consist in a deep inspiration, followed by a convulsive expiration, differing only in degree, the air in the first instance being expelled by the mouth, in the second by both mouth and nares. Sighing and yawning are due to the same cause—want of oxygen in the blood—and differ from each other only in the former being voluntary, the latter involuntary. In both these acts a prolonged and deep inspiration is followed by a quick and usually audible expiration. Laughing and sobbing, though expressing very different emotions, are produced very much in the same way, and are the result of short, quick, convulsive movements of the diaphragm, which are accompanied by the action of the facial muscles producing those changes in the features so characteristic of joy or sorrow. Laughing and sobbing, like yawning, are, so to speak, catching, or contagious. Hiccough is a purely inspiratory act, and consists in sudden convulsive involuntary contractions of the diaphragm, the glottis constricting spasmodically at the same time; the well-known sound is due to the

air striking against the closed glottis. Hiccough is frequently caused by partaking too rapidly of dry food or effervescing and alcoholic drinks, and is not an infrequent symptom of disease.

It is obviously of importance that the number of respirations in a given time be determined as accurately as possible. A great difference of opinion, however, has prevailed, in this respect, among physiologists, Haller,<sup>1</sup> for example, giving twenty respirations a minute as the normal number; Magendie,<sup>2</sup> fifteen; Milne Edwards,<sup>3</sup> sixteen to twenty-two. This disagreement in the result of a mere matter of observation is due, in some instances, to the number of cases examined having been too limited to warrant a general conclusion, and, in others, to influences modifying the number of respirations within the limit of health not having been taken into consideration. The importance of examining a great number of cases before drawing any conclusion as to the average number of respirations per minute is well shown by the observations of Hutchinson.<sup>4</sup> Of 1887 cases examined (Table LIX.), in 561 the number of respirations was found to be twenty per minute; in 239 cases, sixteen per minute; in 79 cases, nine to sixteen per minute. Such a difference in the number of respirations, as observed in these three sets of cases, and also of the remaining ones of the table, prove that there must be numerous conditions influencing the rapidity of the respiratory movements as we have seen is the case with the pulse.

TABLE LIX.<sup>5</sup>—RESPIRATIONS.

| Per minute.       | No. of cases. | Per minute.        | No. of cases. |
|-------------------|---------------|--------------------|---------------|
| 9 to 16 . . . . . | 79            | 21 . . . . .       | 129           |
| 16 . . . . .      | 239           | 22 . . . . .       | 143           |
| 17 . . . . .      | 105           | 23 . . . . .       | 42            |
| 18 . . . . .      | 195           | 24 . . . . .       | 243           |
| 19 . . . . .      | 74            | 24 to 40 . . . . . | 78            |
| 20 . . . . .      | 561           |                    |               |

In a total of these 1887 cases the majority breathed 16 to 24; one-third 20 respirations per minute.

Among these the influence of age is very important, thus, as shown by Quetelet<sup>6</sup> (Table LX.), the number of respirations at birth are more than double the number at twenty years of age, and from this age upward the number of respirations diminishes. It is evident, therefore, that the number of respirations per minute, as deduced from the examination of a number of individuals, will depend, *cæteris paribus*, upon their age; and we should expect to find young persons breathing more rapidly than old ones. It will be readily understood, therefore, why 560 persons, on an average, should be found to breathe twenty

TABLE LX.—RESPIRATIONS AT DIFFERENT AGES.

| Per minute.  | Age.            |
|--------------|-----------------|
| 44 . . . . . | At birth.       |
| 26 . . . . . | 5 years.        |
| 20 . . . . . | 15 to 20 years. |
| 19 . . . . . | 20 to 25 "      |
| 16 . . . . . | 30 "            |
| 18 . . . . . | 30 to 50 "      |

<sup>1</sup> *Elementa Physiologiæ*, t. iii. p. 289.

<sup>3</sup> *Physiologie*, tome ii. p. 480.

<sup>6</sup> Hutchinson, *op. cit.*

<sup>2</sup> *Précis élémentaire de Physiologie*, t. iii. p. 337.

<sup>4</sup> *Cyclopædia of Anat. and Phys.*, vol. iv. part 2, p. 1085.

<sup>6</sup> Quetelet: *Sur l'homme*, etc., 1835, t. ii. p. 84.



times per minute, and 239 persons only sixteen, if the first set examined are, on an average, younger than the second set.

In speaking of the various conditions that modify the number of cardiac beats in a given time, the influence of size was noticed, it being mentioned that the number of cardiac beats in a given time was more numerous in the young and small child, and young and small animal, than in the adult man or large animal. Now, the same relation that we have just pointed out as existing between youth and the number of respirations in man, will also be found to prevail if large animals are compared with small ones, or if the same animal be compared at different ages. Thus, as observed by Milne Edwards,<sup>1</sup> and by the author, while the number of inspirations in the whale is only about four or five in the minute, and in the rhinoceros, hippopotamus, giraffe, and horse ten to the minute, the number of respirations are thirty-five or more in the same period of time in the rabbit and guinea-pig, while, according to Colin,<sup>2</sup> the number of respirations being thirteen to sixteen in the sheep, will be sixteen to seventeen in the lamb; in the cow fifteen to eighteen; in the calf, eighteen to twenty; in an adult dog, fifteen to eighteen; in the young dog, eighteen to twenty. The cause of this difference in the number of respirations, according to the age and size of the animal is, no doubt, due, as in the case of the number of cardiac beats, to the same cause, that of the vital processes generally being more active in small animals than in large ones.

Sex seems to influence but little the number of respirations, no appreciable difference being observed in boys or girls; young men, however, breathe a little more rapidly than young women of the same age. Everyday experience teaches us to what an extent respiration may be accelerated by nervous excitement and exercise. The influence of muscular exertion is not limited simply to active exercise, the mere change from the recumbent to the sitting position, or of standing up, will increase the respiratory movements. Thus, Dr. Guy states that lying down the number of his respirations was 13 per minute, while sitting 19, and when standing up 22. As might be expected, during sleep the number of respirations is diminished, according to Quetelet,<sup>3</sup> the diminution being about 1 in 4, or 25 per cent. It will be seen, from what has just been said, that the number of respirations must vary very much within the limits of health; and that, therefore, only an approximately average number can be ascertained. Of 1887 cases examined by Hutchinson,<sup>4</sup> 1731 breathed from 16 to 24 times, and nearly one-third of them 20 times a minute. The average number of respirations we have found to be from 18 to 20 times a minute, and we may add here, incidentally, that during each respiration there are about four heart beats.

#### MECHANICAL WORK PERFORMED DURING RESPIRATION.

It will be remembered that, in describing the circulation, it was estimated that the mechanical work performed by the heart amounted, in

<sup>1</sup> Physiologie, tome ii. p. 486.

<sup>3</sup> Op. cit., p. 88.

<sup>2</sup> Physiologie Comparée, t. ii. p. 152.

<sup>4</sup> Op. cit., p. 1085.

twenty-four hours, to 128 tons. We shall see, hereafter, in the investigation of the sources of the forces of the body, that it is equally important to determine, as far as possible, the mechanical work performed by the respiratory muscles in the same period of time. This may be estimated, at least approximately, in the same way as in the case of the heart, by multiplying the weight by the height raised. It has already been mentioned that the intrathoracic is less than the extrathoracic pressure, owing to the elasticity of the lungs offering a resistance to the inspired air distending them. It is evident, therefore, that, at each inspiration, the chest lifts so much of the external atmosphere pressing down upon it as is not opposed by the corresponding part of the internal atmosphere, or that part opposed by the elasticity of the lungs. Now the difference between the intra- and extrathoracic pressure, or the excess in weight of the external over the internal air, can be pretty accurately determined by inspiring air out of a mercurial manometer through one nostril, the mouth and other nostril being closed. Let us admit that about 40 cubic inches of air be inspired in this manner, and, with Donders,<sup>1</sup> that 57 mm. of mercury (2.2 inches) be sucked up in the proximal limb of the manometer, and that this represents the excess in the pressure of the external over the internal air; and further, that we add 15 mm. to this on account of the resistance of the lungs, then by multiplying 72 mm. (2.8 inches) by 20 sq. decim. (133 inches), or the area of the thoracic walls, the quotient, 1440 sq. decim., or 194.4 kilom., or about 427.68 pounds, will be the weight in mercury raised by the inspiratory muscles of the thoracic walls. Let us also suppose, with Fick,<sup>2</sup> that in raising this weight the thoracic walls traverse a distance of 0.001 meter (about  $\frac{1}{25}$ th of an inch), then the quotient of 194.4 kilom. by 0.001, or 0.1944 meter kilogrammes (1.4 foot-pounds) will be the work done—that is, the inspiratory muscles of the thorax do an amount of work equal to raising 1.4 pounds through one foot. In the same way, by multiplying the area of the diaphragm 3.5 sq. decim. (about 57 sq. in.) by 82 mm. of mercury, 10 mm. being added to the 72 on account of the abdominal pressure, the quotient, 287 sq. decim., or 38.7 kilom. (about 85.14 pounds), will be the weight raised by the diaphragm. Multiplying the latter, or 38.7 kilom., by 0.114 meter (about  $\frac{3}{10}$ th of an inch), the distance traversed by the diaphragm, the quotient, or 0.44 meter kil. (3 pounds), will be the work done by the diaphragm; and the total work  $0.1944 + 0.44 = 0.63$  meter kil. ( $4 + 3 = 4.4$  foot-pounds)—that is, the work done by the inspiratory muscle, at each inspiration is equal to the work of raising 4.4 pounds through one foot.

It will be observed that, during expiration, the mercury rises higher in the manometer than in inspiration; for example, in an experiment where 2 inches of mercury were elevated in inspiration,  $2\frac{1}{2}$  inches were elevated in expiration; and further, that the difference in the level of the mercury during inspiration and expiration depends upon the depth of the inspiration. It might naturally be concluded, from these experi-

<sup>1</sup> Physiologie des Menschen, Erster Band, S. 419. Leipzig, 1859.

<sup>2</sup> Die Medicinische Physik, S. 209. Braunschweig, 1866.



ments, that the expiratory force was greater than the inspiratory. It will be remembered, however, that expiration is due, not only to the passive relaxation of the inspiratory muscles, but to the active contraction of the thoracic walls, due to their elasticity, which the inspiratory muscles, in dilating the thorax, must overcome, just as the air in entering the lungs must overcome their elasticity. The force of the inspiratory muscles is expended, therefore, not only in elevating the mercury in the manometer, but in overcoming the thoracic elasticity, which amounts to about half a pound (7.8 ounces) on the square inch. It is to this latter force which is due, during expiration, the excess just noticed in the elevation of the mercury in the manometer, and which may be taken as a measure of it. But since this force is overcome by the inspiratory muscles in dilating the thorax, it should be estimated as inspiratory rather than as expiratory power. As in the experiment just performed, the excess of half an inch or more of mercury elevated during expiration is one-fourth that of the two inches elevated during inspiration, one-fourth of the mechanical work performed during inspiration as indicated by the manometer, should be added to the latter, which will make the amount of mechanical work done during each inspiration equal to 5.5 foot-tons, not including, however, the weight of the ribs lifted.

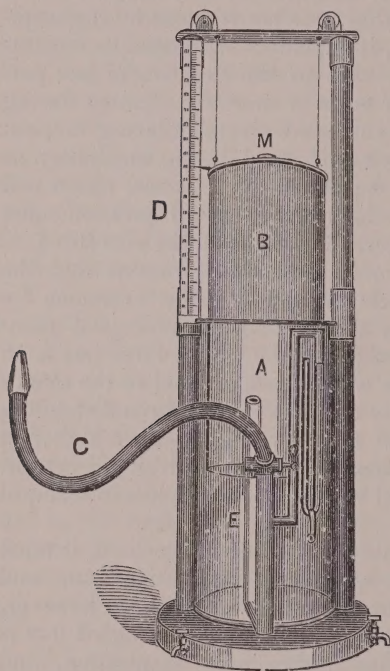
It should be mentioned that it is only in deep inspirations that the opposing force offered by the thoracic walls, and to be overcome by the inspiratory muscles, becomes very apparent in the mercurial manometer. This is as might be expected, since the elastic force put forth by the thoracic walls in their reaction will be proportional to the extent to which they have been stretched by the inspiratory force distending them. It is for this reason that the mercury rises so little higher in expiration than in inspiration in the manometer during tranquil breathing. The mechanical work performed will be, therefore, less in tranquil than in deep inspiration.

It is needless to mention that whatever estimate is accepted, it must vary with the capacity of the chest, number of respirations, etc., and can only be considered as approximately true. Admitting, however, that a mechanical work equal to raising 5.5 pounds through 1 foot is performed by the inspiratory muscles during each inspiration, and supposing further, that the individual inspires 18 times a minute, then 99 pounds are raised 1 foot during a minute, 5940 pounds during an hour, 142,560, or over 63 tons during the day. If, however, the chest be less expanded than we have supposed it to be, and proportionately less mercury sucked up out of the manometer during inspiration, and less expelled during expiration, for example, one-third less, and the number of inspirations be fewer, it is evident that the above estimate will be reduced to about 21-foot tons. Inasmuch as we have seen that expiration is rather a passive than an active process, a return to a condition of equilibrium, the work done by the expiratory muscles was not taken into consideration in the above estimate, and can, for the reason just given, be neglected. If, however, the expiration becomes active and deep, then the work performed may amount, as shown by essentially similar calculation, to nearly as much as that performed during inspiration.

## BREATHING CAPACITY.

On account of the importance of ventilation, of estimating the amount of oxygen absorbed, and carbonic acid exhaled, of determining the amount of heat produced in the body, etc., it is necessary that the amount of air inspired and expired during respiration should be accurately measured. For this purpose we make use of the spirometer. The instrument described by Hutchinson<sup>1</sup>, and somewhat modified by Hawksley for the author, consists (Fig. 246) essentially of a cylindrical

FIG. 246.



Hutchinson's spirometer.

vessel (A), with a capacity of about 7.5 litres (2 gal.), containing water, out of which a receiver (B) can be elevated and depressed by breathing into it through a tube (C), and then the height to which the receiver is elevated and depressed, as shown by the scale D indicating the volume of the air expired and inspired. In using the spirometer, it should be placed upon a firm, level table, about three feet from the ground. The water tap then having been turned off, and the air tap opened, clear, cold water is poured through the spout of the cylindrical vessel A, until it is full, any excess of water running off by the tap in communication with the air tube. Enough colored spirit is poured into the U-shaped tube, until it stands at a level of about 3.5 inches. The counterpoising weights being then suspended within the framework M, and over the pulleys, and the air tap

closed, the instrument is ready for an observation. The person whose breathing capacity is to be determined standing erect with head thrown backward, and loosely attired, applies by the mouth-piece the flexible tube C to his mouth and expires into the spirometer. The air from his lungs passes thence into the tube E, elevating the receiver B, the volume of air expired, expressed in cubic inches, being shown by the number of the scale to which the index connected with the receiver has been elevated. At the termination of the expiratory effort, the air-tap must be closed.

Each division of the scale corresponds to two cubic inches. The descent of the lever through an inspiratory effort, as indicated by the

<sup>1</sup> Op. cit., p. 1069.



scale read in the reverse direction, will give the amount of air inspired. The volume of air must, however, be corrected for temperature, for the temperature of the air will be at once reduced to the temperature of the water in the spirometer, to which it has passed, and which is warm or cold according to the season. Practically the change in the bulk of the air will amount to about  $\frac{1}{500}$  for every degree Fahr., and the difference should be added or subtracted as the temperature of the room in which is the spirometer is below or above  $60^{\circ}$ . Suppose, for example, 295 cub. in. be breathed into the spirometer, the temperature of the room being  $55^{\circ}$ , then 2.9 cub. in. should be added to the 295 cub. in., since  $\frac{5}{500}$  equals  $\frac{1}{100}$  of 295; equals 2.95 cub. in.; on the other hand, if the air be at a temperature of  $70^{\circ}$ , then 5.9 cub. in. should be subtracted from the 295, since  $\frac{10}{500}$  equals  $\frac{1}{50}$  of 295, equals 5.9 cub. in. The U-shaped tube acts as a gauge, since, as long as the colored fluid remains at the same level in its two limbs, the density of the air within and without the receiver is the same, which is necessarily an indispensable condition in the working of the instrument. In order to expel the air from the receiver, and return it to its original position, the plug is removed with one hand, while the receiver is depressed with the other. The experiments having been concluded, and it is desired to empty the water out of the spirometer, it is only necessary to open the water-tap. If a healthy adult breathe easily into the spirometer in the manner indicated, it will be found that usually about 20 cub. in. pass into the instrument with each expiration. If now the air be expelled, and the receiver returned to its original position, and the air-tap be opened, fresh air will pass freely into the receiver, and, the pressure of the air within and without being the same, the receiver will be elevated by the counterpoising weights. Suppose a hundred cubic inches of air have been passed in this way into the receiver, and now a gentle inspiratory effort is made, the receiver will descend, and it will be found that its index has fallen to the number 80 on the scale, showing that 20 cub. in. of air have been inspired. By experimenting in this way upon a number of persons, it will be found that, *cæteris paribus*, on the average, that in easy, tranquil breathing about 20 cub. in. of air are taken into the lungs with each inspiration, and about 20 cub. in. are given out with each expiration. In reality the expired air is about  $\frac{1}{50}$ th to  $\frac{1}{70}$ th less in volume than the inspired air. This is due, as we shall see, to the fact of the carbonic acid excreted being a little less in amount than the oxygen absorbed. The 20 cub. in. of air inspired and expired during each respiration are usually known as the tidal or ordinary breathing air. If now a forcible expiration be made, not only will 20 cub. in. of air pass into the spirometer, as in easy breathing, but as much as 100 additional cub. in. This extra quantity, so to speak, of expired air is not usually changed in respiration, but only when the necessity is felt of more completely renovating the air in the lungs, and is called, therefore, the reserve or supplemental air, and amounts to about 100 cub. in. In prolonged expiratory efforts, such as sneezing and blowing, this reserve air is more or less expelled. As the reserve air is vitiated through continually receiving water and carbonic acid from the blood of the lungs, pearl-divers and others who are in the habit of temporarily arresting

their respiration, instinctively first get rid of their reserve air by forcibly expiring several times, and then fill their lungs with fresh air. If the chest be now enlarged by a forcible inspiration instead of an expiration, the spirometer having been suitably arranged, as much as 110 cub. in. can be withdrawn from the instrument over and above the 20 cub. in. due to an ordinary inspiration. This constitutes what is known as the complemental air, and usually amounts to 110 cub. in. It is drawn upon whenever an effort is made that demands a temporary arrest of respiration, in blowing, yawning, sneezing, etc., to a certain extent in sleep, when the breathing is deep, at the moment immediately preceding some muscular effort, etc. The complemental air can also be indirectly estimated by deducting the sum of the tidal and reserve airs (20 cub. in. plus 100 cub. in.) from the volume of the external breathing air, or that which can be expelled from the lungs by the most forcible expiration after the most profound inspiration, and which, we shall see in a moment, amounts to 230 cub. in.; thus 230 cub. in. less 120 cub. in. equals 110 cub. in. The capacity of the lungs, and the fact that after death they always contain air, make it evident that the air is never entirely expelled, even by the most powerful expiration. A certain quantity of air, therefore, always remains in the lungs. It is known as the residual air, and may be approximately considered as amounting to 100 cub. in. The amount of the residual air cannot be determined directly, either in the living or dead body, since the volume of air within the lungs after an ordinary expiration consists of the sum of the reserve and residual airs. If this, however, can be determined, the deduction from it of the reserve air will give the residual air. Now it is well known that hydrogen gas when inspired is not absorbed by the blood, and that gases will diffuse into each other until the mixture becomes uniform: availing himself of these facts, Grehaut<sup>1</sup> made the subject of his experiments inspire a definite quantity of hydrogen gas until the mixture of hydrogen and air became uniform, and then estimated by analysis of the expired air the quantity of air remaining in the lungs, and necessarily represented by the volume of the hydrogen lost. The amount of air—that is, the sum of the reserve and residual air—in the lungs at the beginning of the experiment can be then easily calculated, and was shown by Grehaut to amount to nearly 200 cub. in. Deducting from this the reserve air, or 100 cub. in., the remainder, 100 cub. in., is the residual air. Assuming the mean capacity of the chest to amount to 312 cub. in., and allowing 100 cub. in. for the heart and great blood-vessels, and 100 cub. in. for the parenchymatic structure of the lungs, there would remain little more than 100 cub. in. for the residual air, which is the estimate given by Hutchinson.<sup>2</sup>

While the method just described gives a sufficiently accurate determination of the respiratory capacity, more exact results are obtained when the tube of the spirometer communicates with a mask closely fitting to the face of the person experimented upon. The mask is provided with two openings furnished with valves working in opposite directions. Through one of the openings the expired air is expelled, while through

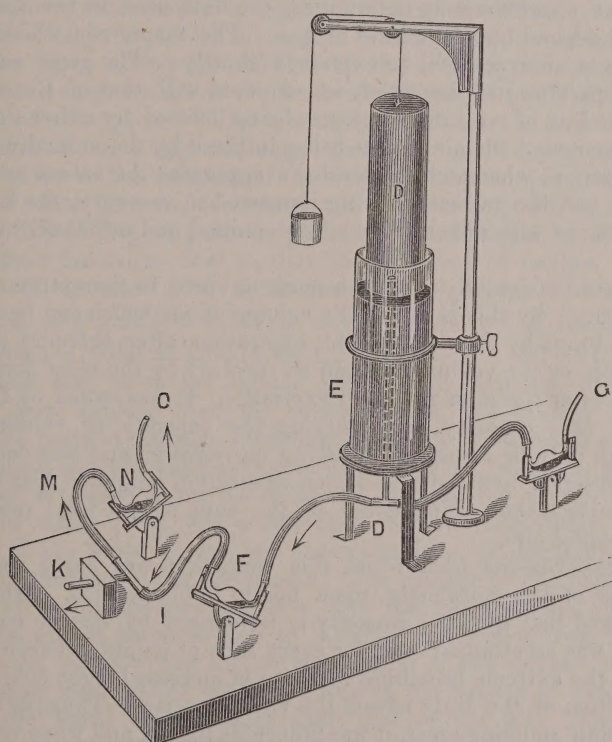
<sup>1</sup> Journal de l'Anatomie, 1864, p. 523.

<sup>2</sup> Op. cit., p. 1067.



the other the air to be inspired passes from the spirometer. A more simple and equally effective apparatus consists of two ivory tubes which are inserted tightly into the nostrils and which connect with a common tube, dividing into two branches; one of these communicates with the spirometer and transmits the air to be breathed, the other allows the expired air to escape. Each of the branches is provided with a valve which opens in opposite directions. According, therefore, to which of the ivory tubes is inserted into the nose the air can be either inspired from or expired into the spirometer. In determining the amount of air inspired or expired by an animal in a given time, we make use of a convenient apparatus constructed for this purpose by Dr. A. P. Brubaker, and which, in principle, is essentially the same as that commonly known as Rosenthal's apparatus. It consists of a small spirometer (Fig. 247),

FIG. 247.



Brubaker's respiration apparatus.

the internal cylinder or gasometer (D) having a capacity of 700 c. cm. (43 in.) and equipoised by a bag of shot. Through the under part of the outer cylinder (E), which is firmly cemented to the stand, passes a T-shaped tube (D) connected with the tubes and valves which transmit the air to and from the gasometer. To one end of the tube (K) passing from the mask closely fitting to the face of the animal is adapted a tube

(I) for transmitting the air to be inspired, and to the other end the tube and valve (M N O) for carrying off the expired air. The valves (F N), just referred to, are the same as those used by Voit in his respiratory apparatus shortly to be described, and consist of oval glass bulbs containing mercury. It is evident that as long as these valves are in the position shown in Fig. 247 the air will only pass in the direction indicated by the arrows. By reversing the valves (F N) the expired air will return back to the spirometer, and so can be measured. In using the apparatus the gasometer must be first raised by the hand through the whole extent or to a given height, the volume of air entering being determined by the scale. As soon as the gasometer has descended by the exhaustion of the air through the inspiration of the animal it must be raised again—that is, if the observation is to last any length of time. By connecting the tube G with a suitable reservoir the animal can be made to breathe any gas that is desired, and the amount inspired in a given time approximately determined, the fluid used in the spirometer will then depend upon the kind of gas. The manner in which the expired gas is analyzed will be explained shortly. The great advantage of the apparatus just described, as compared with that of Rosenthal, is due to the fact of so little resistance being offered by either the valves or the gasometer, the air in fact being inspired by the animal with little or no exertion, whereas in Rosenthal's apparatus the valves used being Muller's, and the gasometer being immersed in mercury, the latter can be only raised with difficulty by a large animal and not at all by a small one.

We have incidentally alluded, a moment since, to the extreme breathing capacity; by this is meant the volume of air which can be expelled from the lungs by the most forcible expiration, after the most profound inspiration, or the volume that can be inspired by the most forcible inspiration after the most profound expiration. It was called by Hutchinson<sup>1</sup> the vital capacity, as signifying the capacity or volume of air which can only be displaced by living movements, and was determined by this observer to amount in a man of medium height (5 feet 8 inches) to 230 cubic inches, being equal to the sum of the tidal reserve and complementary airs.

The experiments upon which this conclusion was based were made by means of the spirometer, upon nearly 5000 persons. Hutchinson also showed that the vital capacity is influenced by various conditions. Thus, it was ascertained that, for every inch of height between five and six feet, the extreme breathing capacity is increased eight cubic inches. The position of the body affects the vital capacity. Thus, in one individual while standing erect, it was 260 cubic inches, and when recumbent it was 230, a difference of 30 cubic inches. The vital capacity is influenced, without doubt, by weight, but, as the weight usually increases with the height, it is difficult to separate the effect of one from that of the other. Age has also an influence, the vital capacity increasing up to the thirtieth year of life, and then diminishing to the sixtieth. The vital capacity is also affected by the sex, being greater, as shown by Herbst,<sup>2</sup> in the

<sup>1</sup> Op. cit., p. 1065.

<sup>2</sup> Meckel's Archiv f. Anat. u. Phys., p. 3, S. 103, 1828.



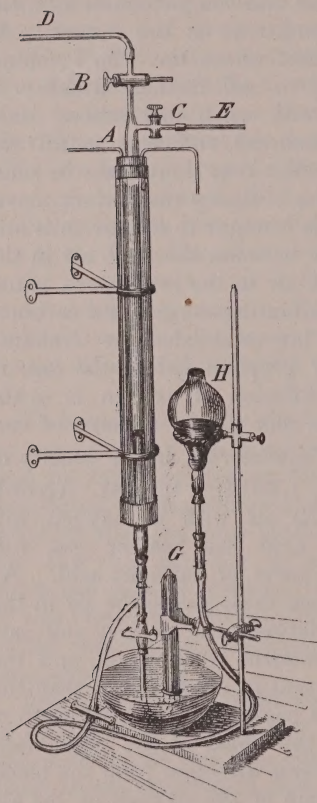
male than in the female. As might be anticipated, any diseased condition affecting the mobility of the thorax or the dilatibility of the lungs, will modify, more or less profoundly, the extreme breathing capacity, hence the importance of the latter as a test of health or disease. Thus, should a person's vital capacity be found to be 190 cubic inches instead of 230 inches, a deficiency of 17 per cent., unless excessively fat, it would be reasonable to suspect in such a person the presence of pulmonary disease; and, yet, in phthisis, the vital capacity may be only 23 inches, the deficiency amounting to 201 inches, or 90 per cent., and yet life be maintained.<sup>1</sup> Inasmuch as the extreme breathing air is made up of the tidal reserve and complementary airs, the latter will be affected by the same conditions as the former. As the effects, however, are less marked than where the whole volume of air is considered, it will be necessary to call further attention to them. When it is remembered that, with each inspiration, only about twenty cubic inches of air are introduced, sufficient to fill the trachea and large bronchial tubes, it is evident that there must be some subsidiary force acting in addition to the ordinary respiratory movements of the chest by which the fresh air is brought to the air cells and the vitiated air expelled. The interchange between the fresh air in the upper part of the lungs and the vitiated air in the lower part, is undoubtedly due to the diffusion of the air containing oxygen and carbonic acid, and which goes on, according to the law established by Graham,<sup>2</sup> that the diffusibility of gases is inversely proportional to the square root of their densities—that is, that the diffusion of oxygen is to the diffusion of carbonic acid as the square root of the density of carbonic acid, or  $\sqrt{1.529} = 1.237$ , is to the square root of the density of oxygen, or  $\sqrt{1.1056} = 1.0514$ , or  $1.237 : 1.0514 :: 95 : 81$ . According to this law, then, the lighter gas, the air, with its oxygen, will descend more rapidly than the carbonic acid, the heavier gas, will ascend, 91 parts of oxygen replacing 81 parts of carbonic acid. As this diffusion is continually going on between these gases, the air in the pulmonary air cells, where the exchange between the oxygen and carbonic acid takes place, has a tolerably uniform composition, and the aëration of the blood is far less intermittent in its character than the respiratory movements of the thorax. The passage of the oxygen from the air of the pulmonary air cells into the blood of the pulmonary capillaries, and of carbonic acid in the reverse direction from the blood into the air, is due to the fact of the tension of the oxygen of the air being higher than that of the blood, and of the tension of the carbonic acid of the blood being higher than that of the air. Necessarily, therefore, the oxygen of the air within the lungs will pass through the wall of the air cell and capillary into the blood, thence into the red corpuscles, combining, as we have seen, with the hæmoglobin of these bodies, while the carbonic acid will pass in the reverse direction from the blood through the wall of the capillary and wall of the air cell into the lungs, and thence out of the body. It is possible that the pulmonary epithelium in acting as a secretory surface may also exercise some

<sup>1</sup> Hutchinson, *op. cit.*, p. 1079.

<sup>2</sup> *Trans. of Royal Soc. Edinb.*, vol. xii, p. 573, 1834.

influence in promoting the absorption of oxygen and elimination of carbonic acid. On the other hand, the oxygen of the arterial blood will readily diffuse through the wall of the capillary into the tissues, the tension of the oxygen in the latter being so low as to amount, practically, to nothing, the oxygen combining in some stable form as rapidly as absorbed. While, owing to the continual production of carbonic acid in some unknown way in the tissues out of the oxygen absorbed, the tension of the carbonic acid of the tissues being always higher than

FIG. 248.



Ærotonometer. (Hoppe Seyler.)

that of the blood circulating in their midst, the carbonic acid will, consequently, diffuse in the opposite direction to that of the oxygen, viz., from the tissues through the wall of the capillary into the blood now become venous through deoxidation of most of its hæmoglobin. The tension of the gases in the blood is determined by means of the ærotonometer. This (Fig. 248) consists of a long glass tube *A*, communicating above by means of the stopcocks *B C* with a tube (*D*), bringing the blood, the tension of whose gases is to be determined, and with one (*E*) leading to the eudiometer for the determination of the gases, and below with a bell-jar (*G*), standing over mercury, and with the reservoir of mercury *H*. The glass tube is first entirely filled with mercury so as to exclude the air, by elevating the reservoir *H*, and is then surrounded by hot water so as to maintain the temperature of the blood examined at that of the animal from which it was drawn. The glass tube *A* is then filled through the depression of the mercurial reservoir with a mixture consisting of known quantities of nitrogen, oxygen, and carbonic acid. The blood being allowed to flow from the artery or vein of the animal for a moment out of the tube *D*, so as to exclude the air, is then diverted

into the gas mixture in *A*. As the blood flows down through the tube into the mercury the mercury is driven up into the bell-jar (*G*), while the tension of its oxygen and carbonic acid are increased or diminished according to the corresponding tension of the oxygen and carbonic acid of the gas mixture, as finally determined by the analysis of the gases in the eudiometer *E*, into which the gases are driven by the elevation of the mercurial reservoir. The general results as to the tension of the oxygen and carbonic acid in the blood, as obtained with the æroto-



nometer by Pflüger<sup>1</sup> and his pupils, Wolfberg,<sup>2</sup> Strassburg,<sup>3</sup> Nussbaum,<sup>4</sup> are as follows:

The tension of oxygen in arterial blood (one atmosphere being equal to 760 mm. of mercury) is equal to 29.6 mm. of mercury, corresponding in amount to 3.9 per cent. of atmosphere, that of carbonic acid being equal to 21.2 mm., corresponding in amount to 2.8 per cent. The tension of oxygen in venous blood is 22.04 mm. of mercury, corresponding in amount to 2.9 per cent., that of carbonic acid being equal to 41 mm. of mercury, corresponding in amount to 5.4 per cent. It is obvious, then, such being the tension of the gases of the blood, that since the tissues offer no resistance to the passage of oxygen from the arterial blood (tension 29.6) into them the tension of their oxygen being practically nothing, and from the fact of carbonic acid being continually produced in the tissues, while the tension of the carbonic acid in the arterial blood is low (tension 21.2), that the oxygen of the arterial blood will pass to the tissues, and the carbonic acid away from them. On the other hand, the tension of the carbonic acid of the air being equal to only 0.38 mm. of mercury, it existing in the atmosphere in the small amount of 0.05 per cent., while the tension of the oxygen of the air amounts to 138 mm. of mercury, corresponding in amount to 20.8 vol. per cent., the carbonic acid of the venous blood (tension 41) will diffuse into the air (tension 0.38), and the oxygen of the air (tension 138) will diffuse into the blood (tension 22.04). The amount of the gases, and the condition in which they exist in the blood have already been considered.

<sup>1</sup> Pflüger's Archiv, Bd. vi. S. 43.

<sup>3</sup> Ibid., Band vi. S. 65.

<sup>2</sup> Ibid., Band iv. S. 465.

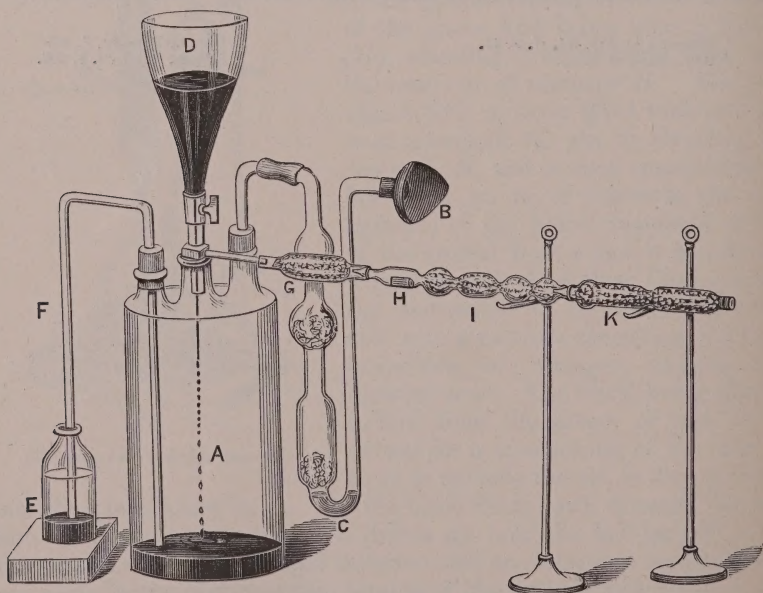
<sup>4</sup> Ibid., Band vii. S. 296.

## CHAPTER XXIX.

### ABSORPTION OF OXYGEN—EXHALATION OF CARBONIC ACID.

HAVING seen that the essence of respiration consists in the absorption of oxygen, and the giving up of carbonic acid, etc., and the manner in which the air containing these gases is respired, it remains for us now to determine, as far as possible, the amount of oxygen absorbed and carbonic acid eliminated by the system in a given time. This is one of the most difficult problems in experimental physiology, and, at the same time, one of the most important, since, as we shall see, all calculations as to the amount of animal heat produced in the body through oxidation and the development of muscular force, etc., are based upon the amount of oxygen absorbed, the carbonic acid and water being exhaled, in a measure of the heat, etc., so produced. Let us endeavor to determine, first, the amount of oxygen absorbed, and then that of carbonic acid, etc., exhaled in a given time. This can be done in several ways,

FIG. 249.



Valentini and Brunner's respiration apparatus.

the simplest of which consists in comparing the composition of the ordinary atmospheric air with that which has been breathed, with the object of determining the amount of oxygen absorbed during one inspiration,



and multiplying this by the minutes, hours, etc., in order to obtain, approximately at least, the amount of oxygen absorbed in the twenty-four hours. The apparatus of Valentin and Brunner, as used by the author for this object, consists (Fig. 249) of a Woulff's bottle A having a capacity of about a litre (61 cub. in.). One of the openings communicates with the mouth-piece B, into which the person expires, the air first passing through pumice-stone and sulphuric acid C so as to dry it. The middle opening communicates with the set of tubes G H I K. H and I contain phosphorus and baryta for the absorption of the oxygen and carbonic acid of the expired air, G and K pumice-stone, etc., that of G for the absorption of the watery vapors that may have escaped, the pumice-stone, etc. in C K for retaining that taken up by the dry air passing through the baryta solution, and which, if lost, would cause an error in the estimate of the carbonic acid exhaled, the tubes being weighed before and after the experiment. Through the middle opening of the Woulff's bottle a funnel (D) provided with a stopcock is introduced, the opening being then hermetically closed. The funnel is filled with a known quantity of mercury. The manner of using the apparatus is as follows: having breathed for say fifteen minutes through the mouth-piece until the air of the Woulff's bottle has been entirely displaced by the expired air, the mouth-piece is entirely closed, any external air being further prevented from passing into the Woulff's bottle by the mercury in E acting as a valve, the air-tightness of the apparatus being assured by the rise of the mercury in the tube F, through the contraction of the expired air in A, consequent upon its cooling and the closure of the tube funnel. The stopcock of the funnel being then turned, the mercury passes into the Woulff's bottle, displacing a known quantity of expired air, the latter passing into the set of tubes G H I K, previously adjusted to the middle opening. The weight of the tubes H and I having been previously determined, their increase in weight will give, respectively, the amount of carbonic acid and oxygen absorbed. Deducting now the amount of oxygen so obtained from the expired air from that contained in an equal quantity of ordinary inspired air, the remainder will be the amount of oxygen retained in the inspiration of such a quantity of air; on the other hand, deducting the trace of carbonic acid usually present in the atmosphere from that obtained from the expired air, and the remainder will be the amount of carbonic acid exhaled into such a quantity of expired air.

The ordinary atmospheric air consists of a mechanical mixture rather than a chemical combination of nitrogen, oxygen, with small amounts of carbonic acid and traces of ammonia, 100 parts, by measure, containing nitrogen 79.19, oxygen 20.81, ammonia 0.04, in round numbers, there being, on an average, 20 of oxygen to 80 of nitrogen. If the expired air, however, be analyzed in the manner just described, it will be found that, as compared with the ordinary air, it has lost oxygen and gained carbonic acid, water, etc. Thus, if an ordinary inspiration be made—that is, 320 c. cm. (20 in.) of air inspired containing 62 cm. (4 in.) of O, and 249 cm. (15 in.) of N, analysis of the expired air, by means of phosphorus or pyrogallie acid, etc., will show that 46.8 cm. (3 in.) of O are returned to the atmosphere, 15.6 cm. (1 in.) of oxygen

having been absorbed by the system—that is,  $\frac{1}{20}$ th of the air breathed represents the amount of oxygen absorbed. On this supposition, about 425 litres (15 cub. feet) of oxygen would be absorbed in twenty-four hours by an adult, as may be seen from the following calculation :

TABLE LXI.

|                                                       |
|-------------------------------------------------------|
| 20 cubic inches of air changed at each inspiration.   |
| 18 respirations per minute.                           |
| <hr/> 360                                             |
| 60 minutes.                                           |
| <hr/> 21600                                           |
| 24 hours.                                             |
| <hr/> 518400 cubic inches of air changed in 24 hours. |
| 1728) 518400                                          |
| 300 cubic feet of air changed in 24 hours.            |
| 20) 300                                               |
| 15 cubic feet of oxygen absorbed daily.               |

Inasmuch, however, as breathing is increased both in rapidity and volume by exercise, it might be naturally inferred that the estimate of the air inspired, and of oxygen absorbed in twenty-four hours, just given, is too low. Such, indeed, is the case, it having been shown by experiment that at least 10,000 litres of air, or about 350 cubic feet, are inspired daily, and 500 litres of oxygen, or 17.5 cubic feet, absorbed—that is, about 20 litres, or 1220 inches, of oxygen, per hour. This last estimate agrees very well with the mean results of Valentin and Brunner,<sup>1</sup> obtained by the above method. These observers determined the amount of oxygen absorbed, by analysis of the expired air in a number of cases, the amount of oxygen present in an equal quantity of inspired air having been previously determined. In the first of these experiments the amount of oxygen absorbed was about 27.12 grammes, 19 litres, and in the second, 33.32 grammes, about 23 litres, per hour. The difference between these two results, as compared with each other, and that we have just given, was probably due to the difference in the number of the respirations, capacity of chest, amount of air breathed, etc. The amount of oxygen absorbed can also be indirectly determined by calculation from the amount of carbonic acid excreted. This method will be explained presently, when we describe the respiration apparatus of Pettenkofer and Voit, for the determination of the carbonic acid, etc., excreted. According to Pettenkofer, the amount of oxygen absorbed per hour was about 23 litres, the same as that determined in the case of Brunner. Whatever the amount may be of oxygen absorbed, whether it be accepted or not, as amounting exactly to 425 litres (15 cubic feet), more or less, in twenty-four hours, it is very evident, and this is the important point, practically, as regards the subject of ventilation, and it cannot be too much insisted upon, that every human being requires an enormous amount of fresh air in twenty-

<sup>1</sup> Valentin: *Lehrbuch der Physiologie des Menschen*, 1847, Band i S. 565, S. 586.



four hours. This is due, not only to the fact that of the air breathed, only one-twentieth represents oxygen absorbed, but also, as we shall see, to the continual vitiation of the air through the carbonic acid and organic matters expired into it, and to the air being then less fit to give up oxygen to the blood and take up carbonic acid from it. While it is quite true that human beings can, apparently, accustom themselves to live in an atmosphere absolutely foul, to breathe over and over again, the same poisonous air, it is only at the expense of their health that this is possible, death resulting sooner or later, from oxygen starvation as surely, though it may be as slowly, as that from ordinary inanition.

We have seen that in ordinary healthy breathing about 10,000 litres (350 cubic feet) of air are inspired in twenty-four hours. The air in a room 7 feet long, wide, and high, and therefore amounting to about 9466 litres (343 cubic feet), would about suffice for furnishing the oxygen required by a human being confined in it for twenty-four hours; and that on the supposition that the air was perfectly pure and fresh. As we shall see, however, double that quantity (20 cub. met., about 650 feet) must be supplied, even per hour, if the air of the room is to be kept in a wholesome condition, free from vitiation by carbonic acid. While, on the average, the oxygen absorbed in twenty-four hours is about what we have estimated, the amount in any given time will vary, being greater or less according to the condition of the digestive system, the external temperature, muscular activity, etc. Thus, during digestion, or if muscular exercise be taken, or the external temperature be lowered, we should expect to find the amount of oxygen absorbed increased, and such is the case, as was shown experimentally by Lavoisier and Seguin<sup>1</sup>, the results of whose observations may be summed up as follows:

1. A man during repose and fasting, the external temperature being 32.5° (90° F.), consumes hourly 24.002 lit. (1465 cub. in.) of oxygen.

2. During repose and fasting, but with the external temperature at 15° (59° F.), he consumes hourly 26.660 lit. (1627 cubic inches) of oxygen.

3. During digestion a man consumes hourly 37.689 lit. (2300 cubic inches) of oxygen.

4. While fasting and raising in fifteen minutes a weight of 7 kil. (about 16 pounds) 343 to a height of 199 in 776 (656 feet) the man consumes hourly 63.477 lit. (3874 cubic inches) of oxygen.

5. During digestion and raising a weight of 7 kil. 343 to a height of 211 inches 146 (700 feet) the man consumes hourly 91 lit. 248 (5568 cubic inches) of oxygen.

It must always be a source of regret that Lavoisier did not describe the apparatus in which he placed Seguin, and by means of which he obtained the results just given. There is not the slightest reason, however, to doubt their accuracy, the genius of Lavoisier being as conspicuously manifested in the disposition of experimental detail, as in the establishment of grand generalizations. In all probability the apparatus used was essentially the same as in the case of the experi-

<sup>1</sup> Mem. de l'Acad. des Sciences, 1789, p. 575

ments performed upon the guinea-pig with the same object, that of determining the amount of oxygen absorbed and carbonic acid exhaled in a given time, consisting in that instance<sup>1</sup> of a bell-jar standing over a pneumatic trough, within which the animal was introduced and supported, after being passed up through the water of the trough, oxygen being introduced as needed, in known quantities, and the carbonic acid exhaled absorbed by alkali. It might be supposed that the results of Lavoisier, just given, would have been shown by more modern methods of investigation, not to be absolutely correct. Even if such should hereafter be shown to be the case, it would not affect the value of the relative results, and that is what is essentially needed for such a comparison as the above. During sleep, as might be expected, the amount of oxygen consumed is considerably diminished,<sup>2</sup> while in hibernating animals, as in the marmot, for example, it is so small that little or no difference can be detected in the composition of the air in which the animal has remained for three hours when in this torpid state.<sup>3</sup> Indeed, according to Regnault and Reiset,<sup>4</sup> only one-thirtieth of the usual amount of oxygen is absorbed by the animal when in this condition. It may be mentioned in this connection, also, that very little oxygen is absorbed by the young of all animals.<sup>5</sup> It has been recently shown by Paul Bert<sup>6</sup> that any increase or diminution in barometric pressure acts upon living beings in increasing or diminishing the tension of the oxygen in the air they breathe, and the blood that circulates through their tissues, and that any increase or diminution in atmospheric pressure is unfavorable to living beings accommodated as they now are, to the present tension of atmospheric oxygen. Indeed, according to this observer, all life perishes in air sufficiently compressed. With a pressure simply of several atmospheres symptoms of narcotic poisoning set in similar to those experienced in breathing an atmosphere containing an excess of carbonic acid, and due probably to the same cause, namely, an excess of carbonic acid in the blood. With still higher pressure, 4 of oxygen—that is, 20 atmospheres, and upward—death takes place from asphyxia, accompanied with convulsions, as when caused by a deficiency of oxygen. Precisely the same effect is caused by the gradual diminution of atmospheric pressure. A sudden diminution, however, causes death probably through the liberation of gases in the blood, which interfere mechanically with its circulation.

As might be expected from the nature of the case, the determination of the amount of oxygen absorbed by a human being in a given time must be of an approximate character. With animals, however, it is different, and especially in the case of small ones, in which the conditions are very favorable, the determination of the oxygen absorbed, as well as the carbonic acid expired, can be most accurately made. The most perfect apparatus for this purpose is that first used

<sup>1</sup> Op. cit., p. 572.

<sup>2</sup> Milne Edwards: *Physiologie*, tome ii. p. 528.

<sup>3</sup> Spallanzani: *Mem. sur la Respiration*, p. 334. Geneva, 1803.

<sup>4</sup> *Recherches Chimiques sur la respiration* Ann. de Chimie, 3d ser, 1849, tome 26, p. 441.

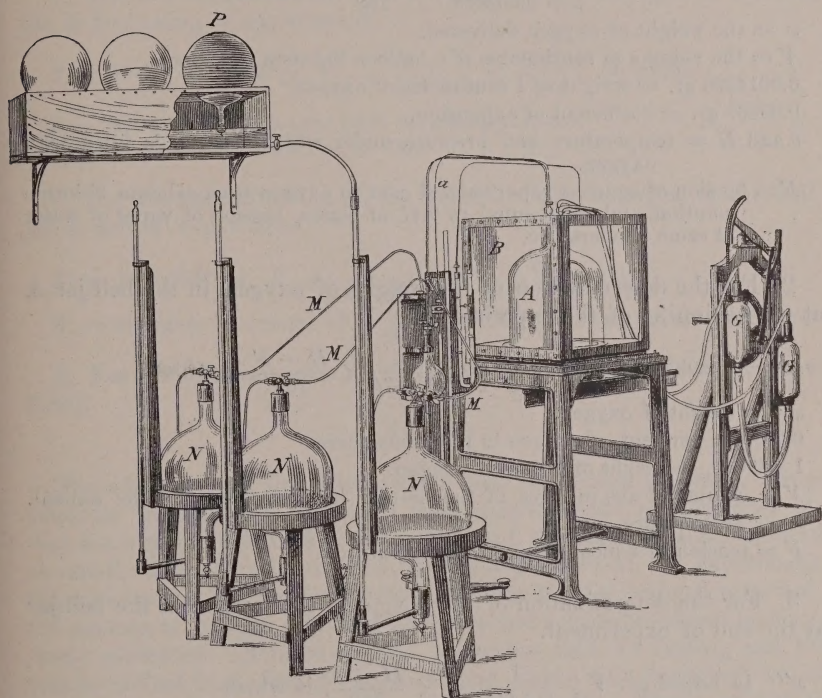
<sup>5</sup> Legallois *Œuvres*, tome i. p. 57. W. F. Milne Edwards: *De l'Influence des agents Physiques sur la vie*, p. 178. Paris, 1824.

<sup>6</sup> *La Pression Barometrique*, p. 1153. Paris, 1878.



by Regnault and Reiset,<sup>1</sup> in their classical researches upon respiration just referred to. It consists essentially of a receiver filled with air enclosing the animal to be experimented upon, and which communicates on the one hand with a reservoir supplying oxygen as fast as it is consumed during respiration, and on the other with an apparatus for the absorption of the carbonic acid exhaled. The detailed disposition of the apparatus, as made for the author by Golaz, of Paris, will be understood

FIG. 250.



Regnault and Reiset respiration apparatus.

from Fig. 250. Within the tubulated bell-jar A, immersed in the cylinder of water B, is placed a little animal, a dog, for example, the subject of the experiment. The animal having been introduced from below, and the opening hermetically closed, the large pipettes G G, filled with a solution of potash or soda of known strength and quantity, and communicating with each other by a caoutchouc tube, absorb and measure the  $\text{CO}_2$  exhaled into the air of the jar A, the air being drawn alternately into the pipettes G G through their elevation and depression by hand or some simple mechanical arrangement. According as oxygen is absorbed by the animal, the gas pressure falls in A, and consequently the oxygen of the balloon N, under the pressure of the calcium chloride solution in P, flows through M, replacing that lost in A. The

<sup>1</sup> Op. cit., p. 299.

object of the gas pipette *a* is to enable the observer to draw a small sample of gas out of *A* for analysis. The temperature being recorded by the thermometer, and the tension by the mercurial manometer, the amount of oxygen absorbed, and carbonic acid exhaled, can be determined by the following formulæ.

1. For the determination of the weight of oxygen delivered from one of the balloons to the jar containing the animal.

$$x = V 0.0014298 \text{ gr. } \frac{1}{1 + 0.00367\theta} \times \frac{H - F}{760}, \text{ in which}$$

*x* = the weight of oxygen delivered.

*V* = the volume in centimetres of a balloon between two marks.

0.0014298 gr. = weight of 1 centimetre of oxygen.

0.00367 gr. = coefficient of expansion.

*θ* and *H* = temperature and pressure under which balloon is filled with oxygen.

*F* = tension of aqueous vapor carried over to oxygen from calcium chloride solution, and about equal to 0.47 of elastic tension of vapor of water at same temperature.

2. For the determination of the weight of oxygen in the bell-jar *A* at the beginning of the experiment.

$$x'' = 0.2095 \times 1.4298 \text{ gr. } V \frac{1}{1 + 0.00367t} \times \frac{H - F}{760}, \text{ in which}$$

*x''* = weight of oxygen.

0.2095 = per cent. of oxygen in the atmosphere.

1.4298 gr. = weight of 1 litre of oxygen.

*V* = volume of air, in litres, of the bell-jar less the volume of the animal.

*t* = temperature.

*F* = tension of aqueous vapor at temperature *t*.

3. For the determination of the weight of the oxygen in the bell-jar at the end of experiment.

$$x''' \text{ to } 1.4298 \text{ gr. } V \frac{1}{1 + 1.00367t} \times \frac{H - F}{760}, \text{ in which}$$

*to* = volume of oxygen in sample of air drawn out of bell-jar through tube at end of experiment, the remaining expressions in the formula being the same as in formula 2.

4. For the determination of the excess in weight of oxygen in the bell-jar, at the end of experiment, over that at the beginning, unconsumed by the animal.

$$x''' - x''$$

5. For the determination of the weight of oxygen (*x*) consumed by the animal.

$$x''' - x'' + b, \text{ in which}$$

*x''' - x''* is as before, *b* the weight of oxygen of the balloons unconsumed at the end of the experiment, *x* being then, as read off on the balloon, the difference in weight between the oxygen at the beginning and end of the experiment.



6. For the determination of the carbonic acid exhaled by the animal.

$$y = 1c \cdot 1.9774 \text{ gr. } V \frac{1}{1 + 0.00367t} \times \frac{H - F}{760} + c, \text{ in which}$$

$y$  = the amount of carbonic acid in the bell-jar at end of experiment.

$1c$  = the volume of carbonic acid in sample of air drawn.

$1.9774$  = weight of 1 litre of carbonic acid, and  $c$  the weight of carbonic acid absorbed by pipettes,  $Vt$ , etc., the same as before.

7. For the determination of the weight of the nitrogen in the bell-jar at beginning of experiment.

$$Z = 0.7905 \times 1.2562 \text{ gr. } V \frac{1}{1 + 0.00367t} \times \frac{H - F}{760}, \text{ in which}$$

$Z$  = nitrogen,  $0.7905$  = per cent. of nitrogen in air.

$1.2562$  = weight of 1 litre of nitrogen.

8. For the determination of the weight of the nitrogen in the bell-jar at end of experiment.

$$Z' = 1n \cdot 1.2562 \text{ gr. } V \frac{1}{1 + 0.00367t} \times \frac{H - F}{760}, \text{ in which}$$

$Z'$  = nitrogen,  $1n$  volume of  $N$  in sample of air drawn,  $Vt$ , etc., as before.

9. For the determination of the weight of nitrogen absorbed or exhaled.

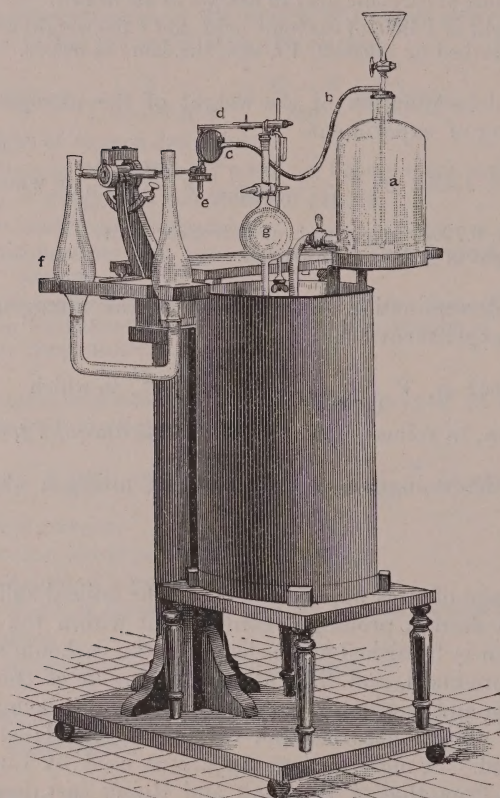
$$Z' - Z.$$

The advantage of this apparatus is that the animal suffers no inconvenience from even a prolonged confinement within the chamber A, that the oxygen is furnished as needed, and the carbonic acid removed as rapidly as produced, and that, at the conclusion of the experiment, the composition and tension of the air within the jar being determined, the amount of oxygen absorbed and carbonic acid exhaled can be accurately estimated. A more modern apparatus used by Ludwig and his pupils,<sup>1</sup> differs from that of Regnault and Reiset just described, not so much in principle as in certain mechanical details. The most noticeable of these is the ingenious contrivance by means of which the oxygen expired passes from g (Fig. 251) into the respiratory tube d, communicating through an air-tight covering with the nostrils of the animal at e, alternately with the passage of the carbonic acid expired into the bulbs f, and which is accomplished through the alternate expansion and contraction of the valve c. For with the rarefaction of the air through inspiration the valve c is drawn away from the end of the tube b, the effect of which is that the air entering the tube b drives the water out of a, which in turn drives the oxygen out of g into the tube d. On the other hand, with the condensation of the air through expiration, the valve c is forced back close to the end of the tube b, the flow of oxygen from the tube d ceases, the carbonic acid exhaled passing into the bulbs f. The amount of oxygen absorbed in a given time by an animal can be

<sup>1</sup> Ludwig's Arbeiten.

also indirectly deduced sufficiently accurately for ordinary purposes from the amount of air inspired, the per cent. of oxygen absorbed having been determined, by Brubaker's apparatus, already described; or directly

FIG. 251.



Ludwig's respiration apparatus.

by connecting the spirometer of that apparatus with a reservoir containing a known weight of oxygen, and filling the cylinder of the spirometer with a solution of calcium chloride instead of water, to avoid absorption the oxygen of the air in the spirometer, etc., absorbed by the animal being replaced by that flowing from the reservoir, and the amount so consumed in a given time at least approximately determined. The amount of carbonic acid exhaled can also be estimated by this apparatus by connecting the expiratory tube with a Pettenkofer tube containing a solution of baryta, and using the volumetric method, as will be explained in a moment. If the air that has been breathed be compared with an equal quantity of atmospheric air, it will be found to differ, not only in having lost oxygen and gained carbonic acid, but in being laden with aqueous vapor, in being warmer, and containing small quantities of ammonia, nitrogen, and organic matters. The determi-



nation of the amount of carbonic acid exhaled in a given time is as important as that of the oxygen absorbed, since the carbonic acid, taken together with the water exhaled, contains the oxygen absorbed by the system during some previous period, and affords the means

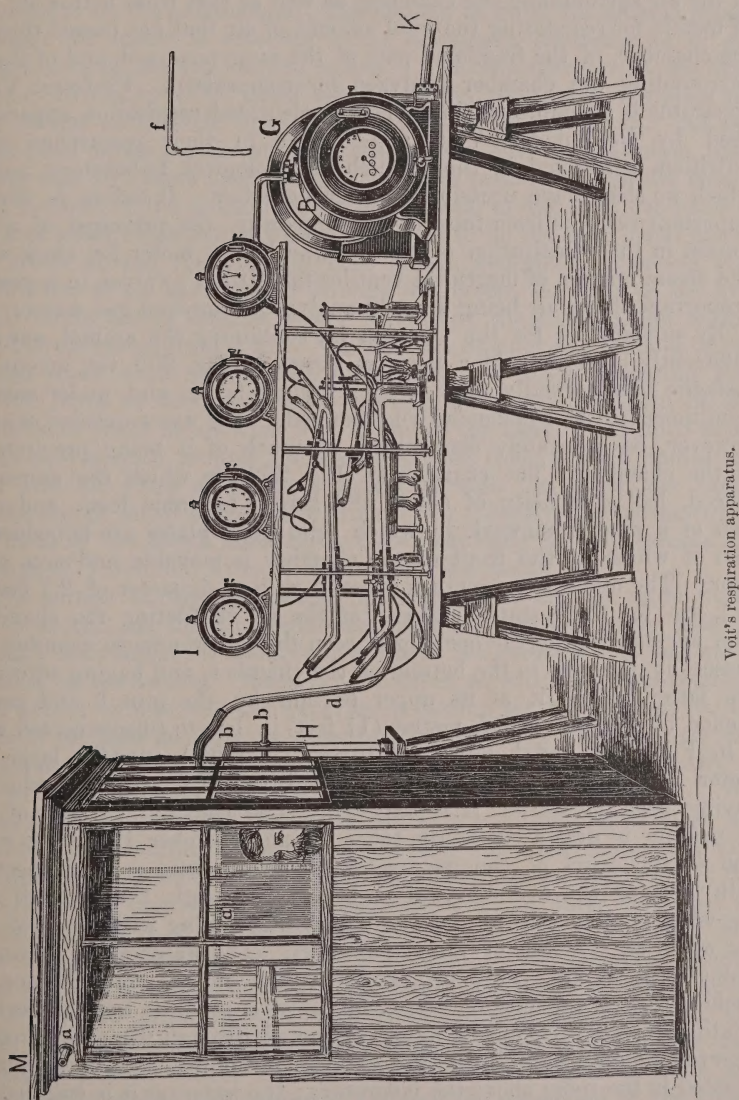


FIG. 252.

Voit's respiration apparatus.

of indirectly estimating the same. We, therefore, usually determine at the same time the amount of carbonic acid and water exhaled by the system, and for this purpose we make use of Voit's respiration apparatus. This consists, as constructed for the author by C. Stollventner and Sohn, of Munich (Fig. 252), of a chamber (H) in which the subject of

the experiment, a large dog, for example, is placed; of a large drum, and pumps worked by a water-wheel for the production of a constant draught of fresh air through the apparatus; of bottles and tubes containing appropriate materials for the absorption of the water and carbonic acid of the air surrounding the chamber, as well as that from within it; and of meters for registering the total amount of air that has passed through the chamber, of the fractional part of the same analyzed, and of the air surrounding the chamber analyzed for comparison. Professor Voit's apparatus is an improved form of the celebrated respiration apparatus, used by Pettenkofer, Voit, and Ranke in their researches upon nutrition, conducted in the Munich Physiological Laboratory, and to which we shall have occasion to refer hereafter. It differs in several important respects from the original apparatus, the principal of which consist in the substitution of a water-wheel as a motor for clock-work and steam engine, of mercurial ventiles for Müller's valves, in a greater proportion of the air being directly analyzed, improved gas meters, etc.

By substituting for the chamber H, containing the animal, one (M) sufficiently large to hold a man, as shown in Fig. 252, the amount of carbonic acid normally exhaled by a human being, and, under various conditions, can be conveniently determined. The water exhaled cannot, however, be accurately determined, so much of it being precipitated in the chamber. The chamber H (Fig. 252), in which the animal is placed, has a capacity of about 380 litres (14 cubic feet), and consists of a zinc framework in which solid glass plates are imbedded, a part of which at the front of the chamber is movable and acts as a door. The other two openings present, with a diameter of 2.7 cm. (1 in.), are for the entrance and exit of the air ventilating the chamber. The air entering by the opening *a*, seen through the large chamber M, passes by the pipe to the bottom of the chamber, and having traversed the latter, leaves it at its upper portion by the pipe *b* and passes thence by the pipe *d* 3.5 metres (11 feet) in length (disconnected with *b* in Fig. 252), and holding 2.4 litres (4.8 pints), into the large gas meter B, having a capacity of 28.57 litres (7.6 gallons), whence, having been measured, it is expelled. The constant current of air so passing is drawn out of the tubes *d* *b* and chamber H by the rotation of the drum of the gas meter B, whose axis is in connection with that of the overshot water-wheel G, through the teeth of the cog-wheel on the axis of the gas meter interlocking with those of the cog-wheel on the axis of the water-wheel. The water-wheel having a diameter of 60 cm. (23.2 in.), and carrying on its circumference 24 buckets with a capacity of 330 c. cm. ( $\frac{2}{3}$  of a pint), is kept uniformly rotating through the fall of water conducted through the pipe *f* from a reservoir holding 1440 litres (360 gallons), not represented in the figure, situated in the room above the laboratory; the water, as it is emptied by the buckets passes into a trough and thence is carried away by the waste pipe K. The flow of water from the pipe *f* can be regulated as to rotate the water-wheel as often as five times per minute. Such a rate, however, is not needed, since with the wheel rotating only once in a minute, or sixty times to the hour, and with an expenditure of 33 litres (8 gallons) of water, over 1700 litres of air pass per hour through the chamber H, or five times as much as we have seen (2857 litres passing through the

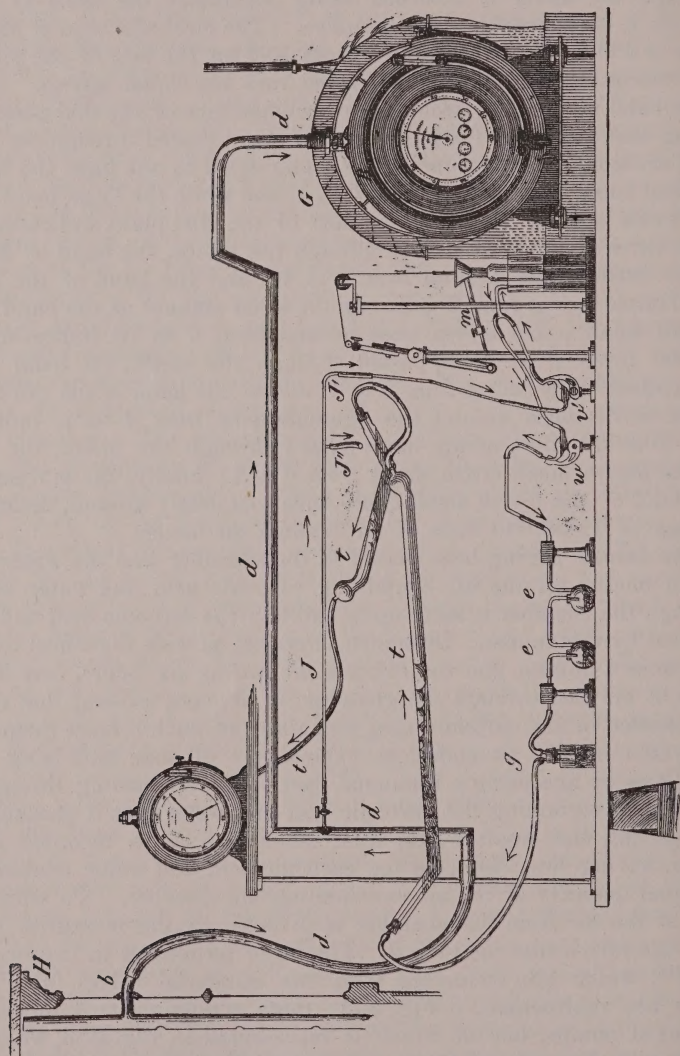


meter with each rotation of the water-wheel) is required in the case of man, and with such a velocity as not to produce a draught (0.36 cm. a second). The velocity of the air through the chamber H during a given time can be always readily determined, when it is remembered that it is equal to the ratio of the amount of air to the sectional area it passes through, or by the animometer. The manner in which the air that passes through the meter is recorded being essentially the same as in gas meters, a brief description will suffice. The circumference of the dial-plate is divided into 100 equal spaces, and on the face of the plate are four circles each circle being divided into ten equal spaces. As the large hand moves once around the circumference of the dial-plate, indicating that 100 litres (200 pints) of air have passed through the meter, each division of the circumference being equal to one litre, the hand of the first small circle moves from 0 to 1, and while the large hand moves ten times around the circumference of the dial-plate, indicating that 1000 litres of air have passed through the meter, the hand of the first small circle moves around from 0 to 10, and the hand of the second small circle moves from 0 to 1. In the same manner as the hand of the second small circle moves once around from 0 to 10, indicating that 10,000 litres of air have passed through the meter, the hand of the third small circle moves from 0 to 1, and as the hand of the third small circle moves once around the circumference from 0 to 1, indicating that 100,000 litres of air have passed through the meter, the hands of the fourth small circle move from 0 to 1; finally, the movement of the hand of the fourth small circle once completely around, records the passage of 1,000,000 litres of air through the meter.

The animal having been placed in the chamber and the water-wheel set in motion, as the air containing carbonic acid and water streams through the chamber it takes up in addition the carbonic acid and water exhaled by the animal. Inasmuch, however, as with the wheel rotating only once a minute and the experiment lasting six hours, over 10,000 litres of air pass through the chamber, it becomes evident that the determination of the carbonic acid and water in such a large quantity of air would involve an enormous expenditure of time and labor. We avoid this by analyzing a fractional part of the air passing through the chamber, determining the carbonic acid and water that it contains and multiplying the result by the total amount of air as recorded by the meter, having first deducted the carbonic acid and water contained in an equal quantity of the air surrounding the chamber. To effect this, part of the air from the chamber is diverted by the mercurial pumps from the tube *d* into the tube *J*. The latter terminates in two branches (*J' J''*) which are connected with two mercurial valves (*v' v''*), the latter not represented in Fig. 253; these communicate with the two mercurial pumps, one of which is represented in Fig. 253, which are alternately elevated and depressed through the movement of the crank *m* connected with the axis of the water-wheel, the one pump rising as the other is falling, and *vice versa*. The pumps communicate also with two other mercurial valves (*w' w''*), the latter not represented in Fig. 253, tilted in the opposite direction to those just mentioned. The air must pass, therefore, always in the same direction, viz., from the

tube *J'* through the valve *v'* into the pump, returning through the valve *w'* into the short bottles *ee* containing pumice-stone and sulphuric acid for the absorption of the water, thence through the large bottles *g* containing water and pumice-stone for resaturation, then through the tubes *tt*, containing a solution of baryta, for the absorption of the carbonic acid, finally escaping by the meters 1 and 2, 2 not represented

Fig. 253.



Illustrating the connection of the tubes with one meter, only lettering same as in Fig. 252.

in Fig. 253, where the amount is measured. As the air passes into the chamber it contains water and carbonic acid. In order to determine the amount of such exhaled by the animal it is necessary to analyze the air surrounding the chamber. This is done in exactly the same way and simultaneously as the analysis of the air within the chamber which we



have just described, the air surrounding the chamber being drawn into a tube by two pumps and through bottles, tubes, and meters similar to those described. Having determined the carbonic acid and water in a given quantity of air surrounding the chamber, this is deducted from the water and carbonic acid of an equal quantity of air that has passed through the chamber, in order to obtain the water and carbonic acid exhaled by the animal. The small gas meters have a capacity of 2.5 litres (5 pints), and the circumference of each is divided into 100 equal parts, each being equal to 25 c. cm. As the large hand moves once around the circumference, indicating that 2500 c. cm. (2.5 litres) have passed through the meter, the small hand moves over one space. It will be also observed that supposing the water-wheel to be rotating once in a minute, that while 25 c. cm. pass out of the small meter 28,570 c. cm. pass out of the large one—that is, 1142 times more air passes out of the large meter than the small one. The amount of carbonic acid and water exhaled by the animal in one hour, as determined by the absorption bottles and tubes, must therefore be multiplied by 1142, and to this must be added the carbonic acid and water remaining in the chamber *H*, tube *d*, and the two meters *I* and *II*, in order to get the total amount exhaled by the animal. The double set of absorbing bottles, tubes, meters, etc., enable us to analyze a definite quantity of two samples of both the air within and without the chamber, and of so obtaining the average amount of water and carbonic acid in a given quantity of inside and outside air. The result of the general investigation will then be more reliable than if the analysis had been confined to a single sample of inside and outside air. Further, to insure success, the gas meters ought to be tested before every experiment. This can be done, as suggested by Voit, by allowing water to flow into a glass vessel of known capacity, the vessel being connected with the meter so that as the air is driven out of the vessel by the water it passes through the meter, or, as is ordinarily done in testing our gas meters, by connecting the upper opening of the meter by which the air usually escapes with a vessel of known capacity containing water. By removing the connecting tube *t'* and allowing the air to enter the meter by the posterior opening, as the water in known quantity flows out of the vessel it is replaced by the air that has passed through the meter. In testing the meters the author has found that there is usually an error of  $\frac{1}{2500}$ th between the absolute amount of air that has passed through the meter and that recorded by it, which must be subtracted from or added to the latter, as the case may be. It might be supposed, from part of the chamber opening and closing as a door, that some of the air containing carbonic acid and water exhaled by the animal might escape through the chinks of the door. The draught of air through the chamber, however, is so great that when a strong-smelling substance is placed within it it is perfectly imperceptible at the door. If any doubt, however, should exist as to the chamber being air-tight, it can be readily made so by filling up the chinks of the door with wax, or a mixture of it. It is very important, also, that the tubing connecting the different parts of the apparatus should be examined in this respect before each experiment.

It remains for us now to describe a little more in detail than we

have done the manner in which the water and carbonic acid are determined by means of the absorbing apparatus. The determination of the amount of water is very simple. The bottles (*e, e*, Fig. 253) through which the air from within and without the chamber passes contain, as already stated, pumice stone and sulphuric acid, which has a great avidity for water. These being weighed in scales, the beams of which oscillate with the addition or subtraction of the  $\frac{1}{750}$ th of a grain, before and after the experiment, the difference will give the amount of water in the air from within and without the chamber; the latter amount, as we have already mentioned, must be then deducted from the former, in order to get the amount of water exhaled by the animal into the fractional part of the air examined. Suppose, for example (see Table of Tabulated Results), of two samples of inside air of 1000 litres each, the mean, or 1000 litres, contained 1.2457 grammes of water, and of equal quantities of outside air, the mean contained 1.1445 grammes of water, the difference, or 0.1012 gramme, would then be the amount of water exhaled by the animal into 1000 litres of air in the given time. The water having been absorbed as the air passes through the bottles the dried air is resaturated as it passes through the bottles *g*, the saturated pumice stone within them giving up the water it contains. Were not the air so resaturated it would take up water from the solution of baryta through which the air next passes, and this must be avoided, as the solution of baryta is used for the absorption of carbonic acid. Of the eight tubes containing the baryta solution, four are large and four are small. The large tubes, through which the air first passes, have a capacity of 460 c. cm. (28 cub. in.), the small ones of 170 c. cm. (10 cub. in.). The tubes are placed somewhat obliquely, in order that the air shall pass as distinct bubbles through the solution, the greatest amount of air surface being, therefore, exposed to the absorbing action of the baryta. The solution of baryta within the two large tubes *t*, only one of which is represented in Fig. 253, receiving the air from the inside of the chamber, is stronger than in that of the remaining tubes, both in the two small succeeding ones and in the two large and two small ones through which the outside air passes. The strong solution of baryta is made by dissolving 21 grammes of baryta in 8 litres of distilled water, the weak one by dissolving 7 grammes of baryta in the same quantity of distilled water. It will be found experimentally, as will be seen in a moment, that about 90 c. cm. and 30 c. cm. of a solution of oxalic acid but recently made by dissolving 2.8 grammes of chemically pure oxalic acid in 1 litre of water will saturate 30 c. cm. of the strong and weak solutions of baryta, respectively. In order to preserve the baryta solution pure it is essential that it should be contained in a bottle, through the stopper of which pass two tubes; through one the solution is drawn out by suction as desired, while by the other tube the air enters, having been freed from its carbonic acid by its passage through caustic soda. It is best to determine the amount of carbonic acid absorbed by the baryta in the case of a small animal. We usually place in the two large tubes 240 c. cm. of the strong solution, and in the remaining six tubes 50 c. cm. of the weak solution, and make use of the method of Pettenkofer, as follows: for example, of the strong baryta, the water having been



introduced into a test tube, or small flask, the solution of oxalic acid is gradually added to it from a finely graduated burette. With each addition of oxalic acid the test-tube is closed with the thumb and shaken. As an indicator of the point of neutralization turmeric paper is used. The paper is dipped into the liquid from moment to moment, ceasing to be browned when the liquid is nearly neutralized; at this instant, a drop of the liquid is placed by means of a glass rod on a strip of the paper, if a trace of alkaline reaction still exists a brown line appears at the periphery of the paper; when this is no longer the case the point of complete neutralization has been obtained. Now suppose, before an experiment with the respiration apparatus it was ascertained by the means just described, that exactly 72.4 c. cm. of oxalic acid neutralized 25 c. cm. of the standard strong baryta solution, it will be found that at the end of the experiment it requires only 61.8 c. cm. of oxalic acid, or 10.6 c. cm. less, to neutralize 25 c. cm. of the strong baryta solution, drawn out of the tubes by means of a pipette. As the carbonic air passes through the latter during the experiment it combines with part of the baryta, and there is, therefore, less baryta to combine with the oxalic acid after the experiment than there was before. Now as for each milligramme of carbonic acid that combines with the baryta during the experiment there will be 1 c. cm. less of oxalic acid required for neutralization after experiment, it follows that 10.6 milligrammes of carbonic acid must have been absorbed by the 25 c. cm. of the baryta solution, since it requires 10.6 c. cm. less of oxalic acid for neutralization after the experiment than before. In other words, the baryta before the experiment combined with 72.4 c. cm. of oxalic acid, after the experiment with 61.8 c. cm., because during the experiment it combined with 10.6 milligrammes of carbonic acid, which are volumetrically equal to 10.6 c. cm. of oxalic acid. As we placed 240 c. cm. of the strong baryta solution in the tube *t*, we must now multiply the 10.6 milligrammes of carbonic acid obtained from the 25 c. cm. by 9.6, in order to obtain the total. The manner of determining the carbonic acid absorbed by the weak solution of baryta being essentially the same as that just described for the strong one, it will be only necessary to refer for details to the Table of Tabulated Results, giving a *résumé* synoptically arranged by Voit of the result of an experiment upon a dog obtained by the respiration apparatus, which we have just described in detail. The carbonic acid exhaled by a human being in twenty-four hours, as determined by the Pettenkofer-Voit's respiration apparatus, amounts, on an average, to 410 litres (25,625 cub. in., or 14 cub. feet) in twenty-four hours.

TABULATED RESULTS OF EXPERIMENT WITH THE PETTENKOFER-VOIT  
RESPIRATION APPARATUS UPON A DOG.

| GAS<br>METERS.         | Amount of air<br>investigated. |          | DETERMINATION OF CARBONIC ACID |                                                               |             |                                                 |                                               | DETERMINATION<br>OF WATER.           |                                       |
|------------------------|--------------------------------|----------|--------------------------------|---------------------------------------------------------------|-------------|-------------------------------------------------|-----------------------------------------------|--------------------------------------|---------------------------------------|
|                        |                                |          | Baryta water tubes. *          |                                                               |             | Carb.<br>acid of<br>air in-<br>vesti-<br>gated. | Carb-<br>acid of<br>1000<br>litres of<br>air. | Water<br>of air<br>investi-<br>gated | Water<br>in 1000<br>litres of<br>air. |
|                        |                                |          | Volumes in<br>c.c.             | Cubic cent. of oxalic<br>acid for 25 c.c. of<br>baryta water. |             |                                                 |                                               |                                      |                                       |
|                        | Revolu-<br>tions.              | Litres.  |                                | Before                                                        | After.      | Differ-<br>ence.                                |                                               | Differ-<br>ence.                     |                                       |
| No. 1<br>Outer air. }  | 26.380                         | 67.108 { | Large 240 c.c.                 | 33.8 c.c.                                                     | 29.8 c.c. } | 0.03900                                         | 0.5811                                        | 0.7682                               | 1.1447                                |
| Small 50 "             |                                |          | Small 50 "                     | 33.8 "                                                        | 33.5 "      |                                                 |                                               |                                      |                                       |
| No. 2.<br>Outer air. } | 26.657                         | 67.024 { | Large 240 c.c.                 | 33.8 c.c.                                                     | 29.8 c.c. } | 0.03900                                         | 0.5819                                        | 0.7670                               | 1.1444                                |
|                        |                                |          | Small 50 "                     | Small 50 "                                                    | 33.8 "      |                                                 | 33.5 "                                        |                                      | 2) 1.1630                             |
|                        |                                |          |                                |                                                               |             |                                                 | 0.5815                                        |                                      | 1.1445                                |
| No. 3.<br>Inner air. } | 22.985                         | 56.044 { | Large 240 c.c.                 | 72.4 c.c.                                                     | 61.8 c.c. } | 0.10236                                         | 1.8264                                        | 0.6947                               | 1.2395                                |
| Small 50 "             |                                |          | Small 50 "                     | 33.8 "                                                        | 33.5 "      |                                                 |                                               |                                      |                                       |
| No. 4.<br>Inner air. } | 25.577                         | 64.981 { | Large 249 c.c.                 | 72.4 c.c.                                                     | 60.3 c.c. } | 0.11636                                         | 1.7907                                        | 0.8135                               | 1.2519                                |
|                        |                                |          | Small 50 "                     | Small 50 "                                                    | 33.8 "      |                                                 | 33.7 "                                        |                                      | 2) 3.6171                             |
|                        |                                |          |                                |                                                               |             |                                                 | 1.8085                                        |                                      | 1.2457                                |

CALCULATION FOR CARBONIC ACID AND WATER.

|                                    | Carbonic acid. |          | Water. |          |
|------------------------------------|----------------|----------|--------|----------|
| In 1000 litres of inner air . . .  | 1.8085         | grammes. | 1.2457 | grammes. |
| In 1000 litres of outer air . . .  | 0.5815         | "        | 1.1445 | "        |
| Difference . . .                   | 1.2270         | "        | 0.1012 | "        |
| In 11600.5 litres of large meter . | 14.23          | "        | 11.74  | "        |
| In 66.55 litres chamber and tube . | 0.11           | "        | 0.07   | "        |
| In 121.02 3d and 4th meters . .    | 0.15           | "        | 0.12   | "        |
| Total . . .                        | 14.49          | "        | 11.93  | "        |

CALCULATION FOR OXYGEN ABSORBED.

| Before experiment.            |  | After experiment.      |               |
|-------------------------------|--|------------------------|---------------|
| Weight of animal 3001.3 grms. |  | Weight of animal . . . | 2987.80 grms. |
| Ingesta . . . 0.0 "           |  | Egesta {               |               |
|                               |  | urine . . .            | 0.0 "         |
|                               |  | feces . . .            | 0.0 "         |
|                               |  | water . . .            | 11.93 "       |
|                               |  | carbonic acid          | 14.49 "       |
| Total 3001.8 "                |  | Total                  | 3014.22 "     |
|                               |  |                        | 3001.30 "     |

The quantity of oxygen absorbed equals the difference, viz. 12.92 "

The proportion of carbonic acid to oxygen, 100 : 89.



This estimate is intermediate between that of Andral and Gavarret,<sup>1</sup> 468 litres (29,238 cubic inches), and that of Edward Smith,<sup>2</sup> 387 litres (24,208 cubic inches), for the same period of time. The experiments of these observers were made with the object of determining only the carbonic acid exhaled, and the apparatus consisted in both instances of a mask closely fitting the face, having two openings provided with valves for the entrance and exit of the air, the carbonic acid exhaled in the experiments of Andral and Gavarret being determined by means of a solution of potash contained in U tubes, and in those of Smith by a solution of potash arranged in numerous layers. The mechanical details of the apparatus made use of by these observers, as well as by their predecessors, Lavoisier and Seguin, Prout, Davy, Dumas, Allen and Pepys, Scharling, and others, not being as perfect as those of the Pettenkofer-Voit respiration apparatus, just described, it would be superfluous to dwell further upon them. In this connection, however, it is proper that some allusion at least be made to the indirect method of determining the amount of carbonic acid exhaled in a given time, so successfully applied in the case of large animals by Boussingault.<sup>3</sup> This method consists of so regulating the diet of the animal experimented upon, a horse or cow, for example, that there is no loss of weight during the experiment, and of weighing everything introduced as food, solid and liquid, and all discharged as urine or feces. Knowing the quantity of carbon entering the body in the food, and leaving it in the urine and feces, the difference between the carbon of the latter and the former (that of the food being in excess) will be the amount of carbon leaving the body by the lungs and skin. As regards the carbon excreted by the skin, it can, for such approximate determinations, be neglected, since, as we shall see, when the skin is considered as a respiratory surface, the carbonic acid exhaled does not amount to more than between  $\frac{1}{50}$ th and  $\frac{1}{200}$ th of the total amount excreted.

<sup>1</sup> Ann. de Chimie et de Physique, 3me serie, t. viii. p. 129.

<sup>2</sup> Phil. Trans., 1859, p. 681.

<sup>3</sup> Mem. de Chimie agricole et de Physiologie, pp. 1-12. Paris, 1854.

## CHAPTER XXX.

### CONDITIONS INFLUENCING PRODUCTION OF CARBONIC ACID, EXHALATION OF WATERY VAPOR, ORGANIC MATTER, AND VENTILATION.

THE amount of carbonic acid exhaled in a given period, like that of oxygen absorbed, is greatly influenced by various conditions. Of the most important of these may be mentioned, the influence of the rapidity of the respiratory movements, sex, age, food, digestion, sleep, exercise, fatigue, temperature, moisture, barometric pressure. Let us consider the influences exerted by the above somewhat in detail. The osmosis of the oxygen of the air and the carbonic acid of the blood within the pulmonary capillaries not being a sudden action, but a continuous one, the amount of the gases so interchanged will naturally depend on the length of time during which the air remains in contact with the respiratory surface; thus, Vierordt,<sup>1</sup> in the experiments performed upon his own person, found that, when he breathed as slowly as possible, 6 per cent of  $\text{CO}_2$  was exhaled in each expiration, but that when he breathed as rapidly as possible only 3 per cent. According to the same authority, if an expiration be divided into two equal parts, the first part will contain, on an average, 3.72 per cent. of carbonic acid, the second 5.44 per cent., the air exhaled during the first period of the expiration containing less carbonic acid than that exhaled during the second period. Vierordt further believes that he has discovered the law by which to calculate the per cent. of carbonic acid contained in an expiration of longer duration, if the duration of the shortest possible expiration, and the per cent. of carbonic acid that it contains are given. Thus, supposing that the duration of the shortest expiration was 0.3125 second, the respirations being 192 per minute, and that this expiration contained 2.8 per cent. of carbonic acid, then an expiration lasting ten seconds, the respirations being six per minute, will contain 5.9 per cent. of carbonic acid. The formula by which this result is obtained is as follows:

$$10 \text{ minus } 0.3125 \text{ equals } 9.6875$$

$$\frac{9.6875}{3.125} \text{ equals } 3.1$$

$$3.1 \text{ plus } 2.8 \text{ equals } 5.9$$

9.6875 being the difference between the duration of the long and short expirations, 3.125 the product of the duration of these two expirations, 3.1 the quotient of the difference of the two expirations divided by the product of the duration of the two expirations, and 2.8

<sup>1</sup> *Physiologie des Athmens*, p. 102. Karlsruhe, 1845.



the per cent. of carbonic acid contained in the short expiration. The quantity of carbonic acid is 2.8 per cent. when the number of respirations is 192 per minute. The latter, when added to the quotient, 3.1, gives 5.9 as the per cent. of carbonic acid contained in the long expiration. Table LXII., synoptically arranged, illustrates the inverse relation existing between the per cent. of carbonic acid in the expired air and the number of expirations.

TABLE LXII.

| Per cent. of CO <sub>2</sub> in expired air. | No. of expirations per minute. |
|----------------------------------------------|--------------------------------|
| 5.9                                          | 6                              |
| 4.3                                          | 12                             |
| 3.5                                          | 24                             |
| 3.1                                          | 48                             |
| 2.9                                          | 96                             |
| 2.8                                          | 150                            |

It does not follow, however, that because the per cent. of carbonic acid contained in each expiration is greater during slow than in rapid breathing that more carbonic acid is expired in a given period in the former case than the latter. On the contrary, the reverse obtains, since the small per cent. of carbonic acid that each expiration contains during rapid breathing is more than compensated for by the greater number of expirations. Thus, suppose, for example, that 250 c. cm. of air are expired six times in a minute, then, as each 100 c. cm. contain 5.9 c. cm. of carbonic acid:  $5.9 \times 2.5 \times 6$ , or 88.50 c. cm., will be the amount of carbonic acid expired in the given time. On the other hand, if the same quantity of air be expired twelve times in a minute, each expiration will contain only 4.3 per cent. of carbonic acid, and yet 129 c. cm. of carbonic acid will be expired in the given time, since  $4.3 \times 2.5 \times 12$  equals 129. The amount of carbonic acid exhaled by an individual depends also upon the sex.

Thus it was shown by Andral and Gavarret<sup>1</sup> that a litre (2 pints) more carbonic acid was exhaled per hour by the male than by the female. Indeed, the difference amounted in some instances to even as much as 7 litres. The difference in the weight of the body was not taken into consideration in the observations of Andral and Gavarret, Scharling<sup>2</sup>, however, found that more carbonic acid was exhaled by the male than the female, even when this was estimated with reference to the body-weight. Apart from the greater muscular activity of the male, as compared with the female, being sufficient to account for the difference in the amount of carbonic acid exhaled by the sexes, other conditions peculiar to the female exert an influence in this respect which must not be overlooked. Thus it was shown by the experiments of Andral and Gavarret, that as long as the menses succeeded each other regularly, the average amount of carbonic acid exhaled remained about the same, being on the average 11.7 litres per hour, with their cessation the amount increased to about 15 litres, while from 60 to 82 years of age it diminished from 13 to 11 litres. Temporary cessation of the menses, whether due to pregnancy or other causes, is

<sup>1</sup> Op. cit.<sup>2</sup> Ann. de Chimie, tome viii. p. 486.

also accompanied by an increase of the amount of carbonic acid exhaled.

As is well known, during the first few hours and days after birth, the infant making little or no movement, sleeping most of the time, generates but little heat, and must, therefore, be carefully guarded against changes in the external temperature. At this early period of life the amount of carbonic acid exhaled must be very small. With the thorough establishment of respiration, this amount is increased, and from the fact of the number of respirations being greater in early than in later life, it is probable that the amount of carbonic acid exhaled, considered with reference to the body-weight, is greater in the infant than in the adult. The necessary data essential for such a comparison are, however, too insufficient to admit of more than the general statement just made. From the observations of Andral and Gavarret<sup>1</sup>, based upon the examination of numerous individuals between the ages of 12 and 102 years, we learn that from the age of 12 to 32, there is an absolute increase in the amount of carbonic acid exhaled, from 32 to 60 years old a slight diminution, and from 60 to 102 years, a very considerable one. The results of the observations of Andral and Gavarret are synoptically arranged in

TABLE LXIII.<sup>2</sup>

| Males.                 |   |    |   | Carbonic acid exhaled per hour. |   |
|------------------------|---|----|---|---------------------------------|---|
| 12 to 16 years of age. |   |    |   | 15 litres (915 cubic inches).   |   |
| 17                     | " | 19 | " | 20                              | " |
| 25                     | " | 32 | " | 22                              | " |
| 32                     | " | 60 | " | 20                              | " |
| 63                     | " | 82 | " | 15.3                            | " |
| 102                    |   |    | " | 11                              | " |

When these observations are supplemented by those of Scharling,<sup>3</sup> we also learn that the amount of carbonic acid exhaled in youth, relative to the weight of the body, is greater than that in the adult, being in the case of a boy, for example, twice as much as in a man. The results of Scharling's experiments might be inferred from those of Andral and Gavarret, since the absolute increase in the amount of carbonic acid exhaled between the period of childhood and adult life, is small, as compared with the increase in the weight of the body within the same period.

As regards the influence of the food upon the exhalation of carbonic acid, the extended series of experiments performed by Dr. Edward Smith<sup>4</sup> upon himself and friends, are very conclusive. Food, with reference to the exhalation of carbonic acid, can be divided, according to Dr. Smith, into two classes, respiratory excitants, which increase the exhalation of carbonic acid, and non-exciters, which diminish it. The excito-respiratory foods include the nitrogenous articles of diet, milk, sugar, rum, beer, stout, the cereals, and potato; the non-exciters, starch, fat, certain alcoholic compounds, the volatile element of wines and spirits, and coffee leaves. The most powerful

<sup>1</sup> Op. cit., p. 129.<sup>2</sup> Op. cit., p. 486.<sup>3</sup> Andral and Gavarret, op. cit., p. 129.<sup>4</sup> Phil. Trans., 1859, p. 715.



respiratory excitants are tea and sugar, coffee, rum, milk, cocoa, ales and chickory come next, then casein and gluten, and lastly gelatin and albumen. The effect of taking respiratory excitants is soon experienced by the system, the maximum effect being usually attained within an hour; their action is of a temporary character, and the effect is not proportional to the quantity taken. Certain respiratory excitants, like tea and coffee, cause an exhalation of carbon in excess of that supplied by these foods, while others, like sugar, cause an evolution less in amount than that supplied. In this connection it may be mentioned that the soothing influence experienced by persons suffering from depression of spirits by drinking tea is probably due to the exhalation of carbonic acid being increased, an excess of carbonic acid in the system giving rise to such feelings. According to Dr. Smith, brandy, whiskey, and gin, the volatile elements of alcohol, gin, rum, sherry, and port wine, when inhaled diminished the quantity of carbonic acid exhaled, while rum and malt liquors, on the contrary, increased the exhalation. While the effect of pure alcohol, according to Prout, Horn, and Vierordt,<sup>1</sup> is to diminish the exhalation of carbonic acid, just the opposite effect is attributed to it by Hervier and St. Leger and Smith. The difference in the result of the effect of alcohol upon the exhalation of carbonic acid observed by these experimenters may be due to the proportion of carbonic acid in the expired air being only considered, and not the absolute quantity exhaled, as was the case in the experiments of Prout, or to the alcohol being administered with or without food, or even to individual peculiarities.

It might be supposed from the fact of the absorption of oxygen being increased during digestion, that the same would prove to be the case with the exhalation of carbonic acid. Such was shown to be the case by the experiments of Lavoisier and Seguin,<sup>2</sup> and in modern times by those of Vierordt.<sup>3</sup> Thus, while during repose and fasting 1210 cubic inches of carbonic acid were exhaled per hour, during digestion this amount increased to 1800 and 1900 cubic inches. Vierordt observed that while, before eating, he exhaled 258 c. cm. of carbonic acid, after eating he exhaled 295 c. cm., or 37 c. cm. more. The reverse effect, or the diminution in the exhalation of carbonic acid in the absence of digestive activity through the depriving one's self, or an animal, of food, was also shown by Vierordt in his own person, and by Spallanzani in the case of snails and silk worms, Marchand in frogs, and Bidder and Schmidt on cats.<sup>4</sup> It has been shown by numerous observers that muscular exertion increases the exhalation of carbonic acid. The experiments of Vierordt, and Edward Smith, in this respect, are especially worthy of mention. According to Vierordt,<sup>5</sup> during moderate exercise the carbonic acid exhaled was increased in amount 1.197 cubic inches per minute, while Dr. Smith<sup>6</sup> found that in walking at the rate of three miles an hour, the exhalation of carbonic acid in one hour was equal to that exhaled during two and three-quarters hours of repose with, and three and one-half hours of repose

<sup>1</sup> Milne Edwards: *Physiologie*, tome ii. p. 536.

<sup>2</sup> *Op. cit.*, S. 98.

<sup>3</sup> *Cyclopedia of Anat. and Phys.*, vol. iv. p. 348.

<sup>2</sup> *Mem. de l'Acad. des Sciences*, 1789.

<sup>4</sup> Milne Edwards, *op. cit.*, pp. 538, 540.

<sup>5</sup> *Op. cit.*, p. 713.

<sup>6</sup> *Op. cit.*, p. 713.

without food. According to the same authority the amount of carbonic acid exhaled during one hour's work on a tread-wheel, was equal to four and one-half hours of rest with, and six hours without food. It should be mentioned that whenever the muscular exertion is, however, excessive, producing fatigue and exhaustion, that the amount of carbonic acid exhaled is diminished, and the same holds true of severe mental as well as of physical work.

A natural inference from that which has just been stated with reference to muscular exertion increasing the amount of carbonic acid exhaled, would be that during sleep the exhalation of carbonic acid should be diminished. The experiments of many observers show that such is in fact the case; thus, according to Dr. Edward Smith,<sup>1</sup> the amount of carbonic acid exhaled during the night, as compared with that exhaled during the day, was in the ratio of 10 to 18. The experiments of Vierordt show that with slight diminution in the external temperature the amount of carbonic acid exhaled by man is increased about one-sixth. Thus the external temperature being between 3 and 15 degrees C. (37.4° and 59° F.), the absolute amount of carbonic acid exhaled per minute was 299.33 c. cm. (about 18 in.), while with the external temperature between 16 and 24 degrees the amount exhaled was only 257.81 c. cm. (15 inches). The result of Vierordt's experiments might have been anticipated, since a fall in the external temperature necessitates a greater production of heat, the high temperature of the body being maintained, and this implies a greater absorption of oxygen and consequently a greater exhalation of carbonic acid. When we come to study the production of animal heat we shall see that one of the most striking contrasts between mammals and birds, as compared with remaining animals, is the power the former possess of generating heat to replace that lost through a fall in the external temperature. On the same principle as that just mentioned we should expect to find also that more carbonic acid is exhaled in winter than in summer, there being a greater demand for the production of heat in the former case than in the latter. This has been shown to be the case more particularly by the researches of Dr. Edward Smith. Thus the maximum amount of carbonic acid is exhaled in January, February, and March, the minimum amount in July, August, and part of September; June and July being months of gradual diminution, October, November, and December of gradual increase. It should be mentioned in this connection, however, that animals, and probably also man, cannot at once adapt themselves as regards their respiration to sudden changes in temperature. Thus it was shown many years ago by W. Milne Edwards<sup>2</sup> that birds, for example, in winter would still consume the same amount of oxygen and exhale the same amount of carbonic acid as usual, though the external temperature was artificially raised to that of summer heat.

It has been shown, especially by Lehmann,<sup>3</sup> that the exhalation of carbonic acid is greater in a moist than in a dry atmosphere. This conclusion was based upon a number of experiments upon birds and

<sup>1</sup> Op. cit., S. 79.

<sup>3</sup> Physiological Chemistry, vol. ii. p. 444.

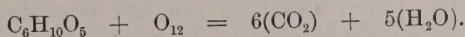
<sup>2</sup> De l'Influence des Agens Physiques sur la Vie. Philadelphia, 1855.



rabbits. Thus rabbits exhaled in a moist air, the temperature being 100° F., 22 cubic inches of carbonic acid, while in a dry air, the temperature being the same, the animals exhaled only about 15 cubic inches.

Finally, it is evident that an increase or diminution in the density of the air inspired, increasing or diminishing the amount of oxygen absorbed, must sooner or later influence the amount of carbonic acid exhaled. Thus, in the experiments performed many years ago by Hervier and St. Leger,<sup>1</sup> it was shown that with a slight augmentation, at least of atmospheric pressure, the amount of carbonic acid exhaled was increased. When the pressure, however, exceeds twenty atmospheres the production of carbonic acid is diminished correspondingly to the diminished oxidation, and with still higher pressure it is entirely arrested, oxidation, according to Bert,<sup>2</sup> as we have seen, ceasing then altogether. With a diminution of atmospheric pressure the amount of carbonic acid produced is also diminished.

Having now considered the amount of carbonic acid exhaled and the various influences modifying the same, let us, in conclusion, study the relation of the carbonic acid exhaled to the oxygen absorbed. Oxygen, as is well known, in combining with carbon to form carbonic acid gas does not change in volume—that is, the volume of carbonic acid gas formed is equal to the volume of oxygen entering into its composition: it follows, therefore, that if all the oxygen absorbed in inspiration combines with carbon to form carbonic acid, the volume of the air expired ought to be equal to that inspired. We have seen, however, that the expired air is from  $\frac{1}{50}$ th to  $\frac{1}{100}$ th less than the inspired air, the difference amounting usually to between 2 and 1 per cent., or, as we have also expressed it, of 100 parts of air respired 5 parts of oxygen are absorbed and 4 parts of carbonic acid are exhaled. It is evident, therefore, that 1 part of the 5 of oxygen absorbed does not combine with carbon to form carbonic acid. What becomes, then, of this one part of oxygen? With what does it combine? Under what form does it leave the body? In speaking of the composition of the carbohydrates, it will be remembered that attention was called to the fact of the hydrogen present being in the proportion to form with the oxygen water. Suppose now that starch, a carbohydrate, be oxidized, the result would be the formation of carbonic acid gas and the setting free of the water, the reaction being as follows:

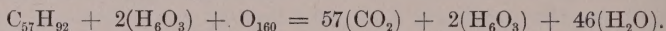


In an animal fed exclusively on starch the volume of carbonic acid exhaled would, therefore, be equal to the volume of oxygen absorbed, since all of the oxygen combines with carbon and reappears as carbonic acid. If, however, the same animal be fed upon a fat in which the hydrogen is in excess, being more than sufficient to form water with the oxygen present, the absorption of oxygen and the oxidation of the fat would result in the formation of carbonic acid and the setting free of the water, as in the first case; but as part of the oxygen absorbed would also combine with that part of the hydrogen in excess

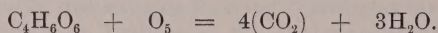
<sup>1</sup> Gazette des hôpitaux, 1849, 3me serie, t. i. p. 374.

<sup>2</sup> La Pression Barometrique, p. 1152. Paris, 1878.

to form water, necessarily some of the oxygen absorbed would not reappear as carbonic acid in the expired air, but as water. The reaction would be as follows, supposing olein to be the fat used :



We would find the same to be the case were the animal fed upon meat, since after the urea was separated from the albumen the remainder of the meat would contain an excess of hydrogen, as in the case of fat, hence part of the oxygen absorbed in respiration would not reappear as carbonic acid but as water, part of the oxygen combining with the carbon to form carbonic acid and part combining with the hydrogen to form water. These theoretical considerations are fully justified by the experiments of Regnault and Reiset. Making use of the respiration apparatus, it was found by these observers that in animals fed upon starch the difference between the amount of oxygen absorbed and exhaled in the form of carbonic acid, was far less in the case of animals fed upon starch than when fed upon fat or meat. Both theory and experiment agree, therefore, in showing that of the oxygen absorbed, that part of it not reappearing as carbonic acid combines with hydrogen and leaves the body as water. On the other hand, when it is remembered that carbonic acid is produced in the system through the decomposition of the carbonates of the blood by the pneumatic acid of the lungs by fermentation, and that in certain kinds of vegetable food, fruits, etc., the oxygen present is in excess, being more than sufficient to form with the hydrogen water, it is to be expected that under such circumstances more oxygen will be exhaled as carbonic acid than can be accounted for by that absorbed in inspiration, as seen, for example, in the oxidation of tartaric acid :



The relation of the oxygen absorbed to the carbonic acid exhaled in respiration is a very complex one, depending upon the nature of the food, the habit of the animal, and various other conditions. While the production of carbonic acid, like that of urea, etc., is, undoubtedly, to a great extent, a process of oxidation, it must be admitted that, as yet, the exact nature of the process has not been determined. It evidently does not take place in the alimentary canal, lungs, or blood, a readily oxidizable substance, for example, like pyrogallie acid, remaining unaffected in the latter, and from the fact that the tissues exhale carbonic acid in an atmosphere of hydrogen or nitrogen, that the formation of the latter is not due to the immediate combination of the oxygen of the air with the carbon of the tissues, the oxygen apparently entering into some molecular combination after absorption by the latter. It can, however, be positively stated that, while food enters the body as such, it leaves it oxidized as carbonic acid, water, urea, etc., and that the oxidation takes place in the tissues, though exactly how, we know not. Some of the intermediate stages in the metamorphosis of food into carbonic acid, urea, etc., have been made out, many yet remain unknown, while the exact reactions and nature of the chemical changes taking place in the tissues are still very obscure.



That the expired air is laden with aqueous vapor becomes evident to every one in cold weather, for, when the external temperature is about  $40^{\circ}$  a distinct cloud is produced by the condensation of the vapor of the breath. Again, the ordinary tarnishing of a surface breathed upon is due to the condensed moisture. It is not to be supposed, however, that the water exhaled from the lungs is entirely due to the combination of hydrogen with oxygen within the system in the manner which we have just described. On the contrary, the greater part of the water exhaled was previously absorbed as such in the form of drinks, etc. Admitting that the part of the oxygen which is absorbed in inspiration, and does not reappear in the carbonic acid exhaled, combines with hydrogen to form water within the economy, the quantity so formed and exhaled is small as compared with the water taken in as drink. For, supposing that the oxygen not reappearing as carbonic acid in expiration amounted in twenty-four hours to about 120 litres, or 168 grammes, the water formed through the combination of the oxygen with the hydrogen of the food, supposing the latter to amount to about 12 grammes, would be 108 grammes, or about 1540 grains:

$$\begin{array}{ccccccc} \text{H}_2\text{O} & \text{H} & & \text{H}_2\text{O} & \text{H} & & \\ 18 & : & 2 & :: & x & : & 12 \end{array} \quad x = 108 \text{ grammes.}$$

whereas the water exhaled from the lungs of a man may amount, in twenty-four hours, to as much as 1200 grammes, or 18000 grains, and more, if exercise be taken. If, however, the available hydrogen of the food amounts to 34 grammes, as is supposed by Dalton,<sup>1</sup> then about 300 grammes of water will be produced in twenty-four hours through oxidation of the former.

It will not be necessary to explain again the manner in which the amount of water exhaled by a man or animal is determined at the present day, the process having been already explained in our account of the respiration apparatus made use of for that purpose. It may be mentioned, however, that Valentin's<sup>2</sup> results, which are often quoted, were obtained by breathing into a curved tube, terminating in Liebig's bulbs, filled with sulphuric acid and pumice stone for the absorption of the water, the increased weight giving the amount of water exhaled. The mean of this experimenter's observations gave a daily exhalation of 540 grammes (8333 grains, equal to about 1.2 pounds) of water, a rather low estimate, but the one usually accepted.

The amount of water exhaled from the respiratory tract will be influenced, as in the case of inert bodies, by the amount of water present in the atmosphere, the temperature, and the pressure. Hence, the dryness of the throat and fauces experienced by persons ascending into high altitudes through the loss of water due to the diminished pressure and great cold. The extent of the respiratory surface will influence also the amount of aqueous vapor exhaled. This is well seen in the diminution of the exhalation in old age, as shown by Barral,<sup>3</sup> the pulmonary cells becoming larger, a less extent of respiratory surface is offered. Finally, the amount of water exhaled is increased

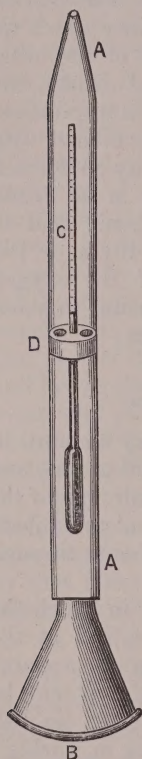
<sup>1</sup> Physiology, 1882, p. 37.

<sup>2</sup> Lehrbuch, Band i. S. 527.

<sup>3</sup> Ann. de Chimie, 1849, 3me ser. t. xxv. p. 166.

by the quantity of water taken in as drink, etc., and by the frequency of the respiration. In conclusion, it should be remembered that, if the ordinary conditions prevailing be reversed, water may be absorbed by the respiratory surface instead of being exhaled. The sudden gain in weight frequently observed in individuals who had not partaken of solid or liquid food, often referred to by writers on physiology<sup>1</sup> is due, no doubt, to absorption by the lungs of the watery vapor of the atmosphere, rather than to cutaneous absorption, as sometimes supposed.

FIG. 254.



Apparatus for determining temperature of expired air.

It has already been mentioned that the expired differs from the inspired air, not only in containing carbonic acid and water, but in being warmer, and containing small quantities of ammonia, nitrogen, and organic matters. Thus, according to Grehant<sup>2</sup>, one of the latest observers, the temperature being at 72° Fahr., and the air inspired by the nares, that exhaled by the mouth had a temperature of 95° Fahr., as determined by a thermometer (Fig. 254, C) placed within the apparatus A, through which the air was expired, and which was uninfluenced by the external temperature. When the air was, however, inspired by the mouth, the air expired had a temperature of only 93°. The result of Grehant's observations differ a little from those of Valentin,<sup>3</sup> previously made. According to the latter observer, the external temperature being at 68°, that of the expired air was 99°. The temperature of the surrounding atmosphere has an important influence on that of the expired air, thus, according to Valentin, in winter, the external temperature being at 18°, that of the expired air was only 85.5°.

Ammonia is undoubtedly exhaled from the lungs, being almost invariably found in the expired air. In fact, it is only absent at certain periods of the day, or during cold weather, as noticed by Richardson.<sup>4</sup> In certain conditions of the system, as in cases of uræmic poisoning, the amount of ammonia in the expired air is so great as to become very perceptible to the patient.<sup>5</sup> At one time a difference of opinion prevailed among physiologists as to whether nitrogen was absorbed or exhaled during respiration. The researches of Regnault,<sup>6</sup> Boussingault,<sup>7</sup> and Barral,<sup>8</sup> leave no doubt, however, that, in mammals and birds at least, under ordinary circumstances, a small quantity of nitrogen is exhaled in respiration, equal to about one-fiftieth by weight of the oxygen absorbed. The reverse, however, appears to be the case with fishes, according to

<sup>1</sup> Carpenter's Physiology, p. 494.

<sup>2</sup> Journal de l'Anat. et de la Phys., 1864, tome i, p. 546.

<sup>3</sup> Physiologie, Band i. S. 533.

<sup>4</sup> The Cause of the Coagulation of the Blood, p. 360. London, 1857.

<sup>5</sup> Lehmann: Phys. Chem., vol. ii, p. 434. Philadelphia, 1855.

<sup>7</sup> Chimie Agricole, pp. 1-24. Paris, 1854.

<sup>6</sup> Op. cit., p. 510.

<sup>8</sup> Op. cit., p. 129.



Humboldt and Provencal,<sup>1</sup> nitrogen being absorbed by those animals. In speaking of nitrogen, it may be incidentally mentioned that its mixture with oxygen as the air we breathe is obviously of advantage, since, on account of its great diffusibility, the air vitiated with carbonic acid is readily renewed during respiration. A small quantity of organic matter, the nature of which is not thoroughly known, but, as we shall see, is, to a great extent, poisonous in character, is constantly present in the expired air. The presence of this organic matter can be shown through the putrefaction of the aqueous products of the expired air when condensed in a cool receiver, or through the putrefaction of a sponge saturated with the vapors exhaled by the lungs.

Many articles of food, like onions, garlic, alcohol, spirits of turpentine, drugs like camphor, musk, asafoetida, when absorbed by the blood and vaporized in the system, are exhaled by the lungs, being readily recognized by their odor in the expired air. That poisonous gases are also exhaled by the lungs is rendered very probable by the experiments of Bernard<sup>2</sup> and Nysten,<sup>3</sup> in which sulphuretted hydrogen and carbonic oxide, so fatal when inhaled, were injected into the veins without bad effect, being eliminated by the lungs as rapidly as they were taken up by the venous blood.

Many animals in which the respiration is of a feeble character, such as slugs, snails, certain kinds of fish, frogs, etc., continue to live in air from which the oxygen has been removed to a considerable extent.<sup>4</sup> Such, however, is not the case with animals whose respiration is very active, as in man. Any considerable diminution in the amount of oxygen in the surrounding air soon causes death. Just as a lamp goes out when the air feeding it does not contain more than about 17 per cent. of oxygen, so with the lamp of life is its flame too dying out, respiration soon ceasing, if the amount of oxygen usually present in the atmosphere be diminished by absorption, or through dilution with some indifferent gas. In fact, air which has been breathed by man once should not be breathed again; such air having lost 5 per cent. of oxygen and gained 4 per cent. of carbonic acid, if breathed twice, will give up but little oxygen to his economy. Indeed, as shown by Lavoisier,<sup>5</sup> air, having lost about 10 per cent. of oxygen, becomes absolutely irrespirable. Such is found to be the case in certain parts of mines where the air contains only that amount of oxygen. It is well known, also, that birds and mammals will suffocate in an atmosphere in which the amount of oxygen has been diminished to that extent. Thus, a mouse will die in six minutes, if confined in such an atmosphere, and a sparrow in an hour, if the oxygen be diminished to half that amount, or 5 per cent. It is not, however, the want of oxygen alone that causes death in breathing bad air, but the simultaneous increase of carbonic acid as well. The effects of an accumulation of carbonic acid in the air, while no doubt often exaggerated, are nevertheless injurious in many ways indirectly, since the oxygen to be absorbed will be diluted by it, and the exhalation of the carbonic acid will be interfered with, a condition of equilibrium

<sup>1</sup> Milne Edwards: *Physiologie*, tome ii. p. 599, note.

<sup>2</sup> *Substances Toxiques*, p. 58. Paris, 1857.

<sup>3</sup> *Recherches de Physiologie*, p. 81.

<sup>4</sup> Milne Edwards: *Physiologie*, tome ii. p. 626.

<sup>5</sup> *Deuxième Mémoire sur la respiration* mem. de Chimie, t. iv. p. 22.

being brought about, and directly by its effects upon the economy giving rise to malaise, headache, a sense of oppression, and even stupor.<sup>1</sup> The ill effects of breathing vitiated air appear, however, in many cases to be due not so much to the carbonic acid as to the organic matter that it contains, and to which we have already referred. According to Foster,<sup>2</sup> while an atmosphere containing simply 1 per cent. of carbonic acid, the oxygen being diminished to the same extent, has little or no effect upon the economy, air containing 1 per cent. of carbonic acid and organic matter that has been exhaled is highly injurious; in fact, according to Pettenkofer,<sup>3</sup> such air becomes unendurable. As we have already seen, the amount and nature of this organic matter are comparatively unknown, the per cent. of carbonic acid exhaled with it is conveniently taken as its measure. Good air, in fact, should never contain more than one-fifth of one per cent. of carbonic acid; and indeed, if the air is to be kept perfectly wholesome, the amount of carbonic acid should never be allowed to exceed even one-tenth of one per cent.; the air of chambers in which animals have breathed beginning to smell even when the carbonic acid present amounts to so little as one part in a thousand of air.

On the supposition that each human being exhales 20 litres of carbonic acid in an hour (Pettenkofer), it is obvious that if the carbonic acid of the surrounding air is not to exceed one-tenth per cent. in amount, that at least 20,000 litres, or 20 cubic metres, of air must be supplied for each person in that period of time, or 480 cubic metres—about 16,800 feet in twenty-four hours.

While a room having a capacity of 343 cubic feet, as we have seen, contains about enough air to supply the oxygen required by a man in twenty-four hours confined in it, such a room would evidently not contain enough air to keep the proportion of carbonic acid exhaled into it in that time in the proportion of one-tenth per cent. A room 25 feet long, wide, and deep—that is, with a capacity of 15,000 cubic feet at least—is necessary.

In breathing in the open, where the atmospheric air is out of all proportion to that expired by any one individual, at no moment is any want of fresh air experienced. In our dwellings also, if properly constructed, a due supply of fresh air is maintained by the opening of windows and doors, and the entrance of the outside air through the cracks, crevices, etc. In churches, theatres, lecture-rooms, barracks, prisons, hospitals, etc., however, where large numbers of people are congregated together, the proper supply of fresh air should never be left to chance. Indeed, this is now so well understood that in the ventilation of such buildings as the Chamber of Deputies and many of the hospitals in Paris, in the House of Commons in London, in the Philadelphia Academy of Music, etc., the air is continually renewed by means of fans worked by engines, etc., regard being paid to the fact that the air supplied is in reference not only to the amount of oxygen to be inspired, but also to the carbonic acid, organic matter, etc., exhaled to be carried away, care being taken that the expired air does not mix with that to be inspired, and at the same

<sup>1</sup> Milne Edwards, *op. cit.*, p. 639.

<sup>3</sup> *Med. Times and Gazette*, 1862, p. 459.



time that drafts be avoided, the velocity with which the air passes through the chambers not being greater than from two to three feet per second. That it is the want of oxygen, however, and not the excess of carbonic acid, that constitutes the natural stimulus to healthy respiratory movement can be shown in two different ways.

First. If an animal be made to breathe an atmosphere of nitrogen into which the carbonic acid exhaled will readily diffuse, the blood being rid, therefore, of any excess of carbonic acid, the breathing, nevertheless, at once becomes difficult, dyspnœa sets in, and death from asphyxia, preceded by convulsions, soon follows.

Second. If the blood of the animal be saturated with oxygen, which can be readily done by artificial respiration, apnœa results—that is, all respiratory movements cease, the condition of the animal, however, in other respects, being perfectly normal. It is evident, therefore, that, in the first case, it is the want of oxygen that gives rise to the dyspnœa, respiratory movements, etc.; whereas, in the second case, the oxygen being in excess, no necessity exists for such respiratory movements, hence their absence; or, on the other hand, if an animal be made to breathe an atmosphere containing an excess of carbonic acid, but, at the same time, plenty of oxygen, though the breathing becomes deeper and quicker, and while there is an excess, even of carbonic acid, in the blood, nevertheless no convulsive asphyxia follows. On the contrary, the breathing soon becomes slower, a state of unconsciousness sets in, and death takes place, as if caused by narcotic poisoning. There can be no doubt, therefore, that the violent respiratory movements preceding death from asphyxia are due primarily to the blood being insufficiently oxygenated, and not to an excess of carbonic acid, any influence exerted in this respect by the latter being of a secondary character, mechanically, for example, in preventing the access of the oxygen, etc. As dyspnœa, apnœa, and asphyxia are rather subjects of study for the pathologist than for the physiologist, I have only incidentally alluded to those conditions so far as they seem to elucidate the relative rôle that oxygen and carbonic acid play as stimuli to the respiratory movements. Inasmuch, however, as the condition of asphyxia is an interesting and important one from many points of view, a brief description of it may not appear inappropriate.

Asphyxia, from *a*, primitive, and *σφνξις*, the pulse, literally a state of being without pulse, the condition brought about when the system is deprived of a due supply of air, whether suddenly by occlusion of the trachea, as in strangulation, or by slow suffocation through breathing in a confined space, manifests itself first by the breathing, both inspiratory and expiratory, becoming more frequent and deeper. This exaggeration of the breathing, or hypernœa, is soon succeeded by a condition of difficult breathing, or dyspnœa, the respiratory movements, at the same time, having become almost entirely expiratory in character, every muscle being brought into play that can contribute in any way to this effect. Sooner or later, the muscles of the whole body become involved in the convulsive expiratory movements that follow. General convulsions then set in, which, after lasting a short time, are followed

by a stage of tranquillity due to exhaustion. At this stage the pupil is insensible to light, the cornea fails to respond to touch, breathing has become almost entirely inspiratory, and occurs only at long intervals. Finally, with a long and deep gasp death takes place, with the head thrown back, nostrils dilated, opened mouth, straightened trunk, and extended limbs. That the convulsions, which occur as dyspnoea passes into asphyxia, are due to the stimulation of the respiratory centre of the medulla oblongata by the insufficiently arterialized blood circulating through it, is proved from the fact of such convulsions being absent if the spinal cord has been previously divided below the medulla, but being present if the part of the brain lying above the medulla only be removed. That these convulsions are, in fact, due to influences emanating from the medulla is still further shown by the rise in blood pressure that occurs during the development of asphyxia, and which is due to the constriction of the arterioles through the stimulation of the vasomotor centre by the excessively venous blood, and by the fact that if the supply of blood to the brain be cut off by ligation of the vessels, convulsions, similar to those observed in asphyxia, follow. The facts just mentioned will become more significant, however, when the structure of the medulla, and its influence upon the respiration and the circulation, have been considered.

Owing to the constriction of the vessels at the periphery that obtains in asphyxia, offering an obstacle to the flow of the blood from the heart, while the increased respiratory movement favors the flow toward it, the heart soon becomes distended, and, finally, exhausted, though continuing to beat for a few moments after respiration has ceased. During the latter stage of asphyxia the blood pressure, therefore, not only falls, but the heart is weakened—that is, unable to empty itself of its contents. Hence, in post-mortem examinations of cases of death from asphyxia, if made before rigor mortis has set in, all the cavities of the heart will be found choked with blood. With the setting in of rigor mortis, however, the blood is expelled from the left side of the heart, the right remaining gorged with venous blood. The difference of opinion, that sometimes prevails, as to whether all the cavities of the heart are filled with blood in death from asphyxia, may be due, therefore, to the length of time intervening between death and the making of the post-mortem examination, having been different in the cases investigated. In this connection it may not be without interest to mention that Harvey<sup>1</sup> notices that, in cases of death from ordinary causes, the left side of the heart and arteries are found empty; whereas, in sudden death, as from syncope or drowning, the arteries, as well as the veins, are found full of blood. The duration of asphyxia varies very much in different animals, and according to the age of the animal. Thus, a dog will be asphyxiated by occlusion of the trachea in four or five minutes, a rabbit in three or four minutes; whereas, as shown long ago by Buffon,<sup>2</sup> puppies just born can be submerged in warm milk for half an hour at a time, several times in succession, and yet recover; while,

<sup>1</sup> Works, p. 115. London, 1847.

<sup>2</sup> Natural History, vol. iii. p.337. London, 1797.



according to Legallois,<sup>1</sup> newborn rabbits lost consciousness only after having been kept thirteen minutes under water. Milne Edwards<sup>2</sup> refers to cases, interesting from a medico-legal point of view, where infants born asphyxiated were revived seven and even twenty-three hours afterward. The remarkable power that animals just born exhibit in resisting asphyxia depends principally upon the demand for oxygen being so slight at this time. In fact, at this early period of existence the newborn mammal is essentially a cold-blooded animal, it depending for its heat almost entirely on external warmth, the blood is still mixed through the foramen ovale being open, the circulation and respiration have not assumed the important *rôle* that they play in the adult, little or no muscular exercise is taken, most of the time being passed in sleep, hence but little oxygen is required. The connection between the deficiency in the circulation and the want of aëration, just referred to, is also seen in cases of syncope in the adult, it being well known that a person in that condition can resist for some time the effects of asphyxia, the amount of oxygen consumed by the tissue being, of course, less in proportion as the circulation is slowed, the oxygen inspired will last, therefore, longer than usual.

<sup>1</sup> Œuvres, tome premier, p. 58. Paris, 1830

<sup>2</sup> Op cit., p. 559,

## CHAPTER XXXI.

### ANIMAL HEAT.

ONE of the most striking phenomenon in the life of man, and in that of the hot-blooded animals generally (mammals and birds), and of plants, also, to a certain extent, which did not escape the attention of the ancients, is the almost constant temperature maintained by the body, notwithstanding the great extremes in temperature to which it may be subjected. Thus, whether one lives in a changeable climate, or passes from the genial atmosphere of the temperate regions into the extreme heat of the tropics,  $53.3^{\circ}$  C. ( $130^{\circ}$  F.),<sup>1</sup> on the one hand, or into the intense cold of the arctics,  $-57.7^{\circ}$  C. ( $-72.5^{\circ}$  F.)<sup>2</sup> on the other, the temperature of the body varies, as we shall see, but little. If, however, the so-called cold-blooded animals, frogs, for example, be observed in this respect, a most notable difference becomes at once apparent, their temperature being, according to the circumstance, higher or lower than that of the surrounding water or air, and any rise or fall in it depending upon that of the latter. Thus, according to Landois,<sup>3</sup> the temperature of the water in which the frog is immersed being successively  $2.8^{\circ}$ ,  $20.6^{\circ}$ , and  $41^{\circ}$  C., that of the stomach of the animal will be respectively  $5.8^{\circ}$ ,  $20.7^{\circ}$ ,  $38.0^{\circ}$  C., while if the animal be living in air at a temperature of  $5.9^{\circ}$ ,  $19.8^{\circ}$ , and  $40.4^{\circ}$  C., that of the stomach will be at  $18.6^{\circ}$ ,  $15.6^{\circ}$ ,  $31.7^{\circ}$  C. Thus, as Hunter expressed it, warm-blooded animals have a certain permanent heat in all atmospheres, while the temperature of cold-blooded ones is variable with every atmosphere, hence the distinction of pomiothermal and poikilothermal animals introduced by Bergman<sup>4</sup>, and which being based upon the relation of the temperature of the body to that of the surrounding medium is a better one than that of hot- and cold-blooded animals, and which we have just incidentally alluded to.

The following table was drawn up from the observations of Davy,<sup>5</sup> Martine,<sup>6</sup> Prevost,<sup>7</sup> and Dumas de la Roche,<sup>8</sup> Jones<sup>9</sup>, Valentin,<sup>10</sup> Hunter,<sup>11</sup> and of the author. When not otherwise mentioned, the temperature in the vertebrates was taken in the rectum.

As the temperature differs often in individuals of the same species, and according to the biological conditions influencing the animal at the moment of observations, and further, as the number of observations are comparatively limited, any results, such as exposed in Table LXIV., can only be accepted as approximately giving the average temperature in animals.

<sup>1</sup> Jameson : British India, vol. iii. p. 170.

<sup>2</sup> Physiologie, S. 393. Wien, 1883.

<sup>3</sup> Recherches Phys. and Anat., p. 161. London, 1839.

<sup>4</sup> Annales de chim. et de phys., 2e serie, t. xxiii. p. 64, 1823.

<sup>5</sup> Journal de physique, lxxi. p. 298, 1810.

<sup>6</sup> Investigations, Chem. and Physiol., Smith. Contrib., 1856.

<sup>7</sup> Repertorium für Anat. und Phys., Vierter Band, S. 359. Bern, 1839.

<sup>8</sup> Works, ed. by Palmer, vol. iv. p. 147. London, 1835.

<sup>9</sup> Erman : Siberia, vol. ii. p. 369.

<sup>10</sup> Gottinger Studien, Abth. i. S. 595.

<sup>11</sup> Essays, Medical and Philos., 1740, p. 337.



TABLE LXIV.<sup>1</sup>—TEMPERATURE OF ANIMALS.

| Name of animal.        | Temperature.                        | Observer.                          |
|------------------------|-------------------------------------|------------------------------------|
| <i>Aves</i> —          |                                     |                                    |
| Chicken,               | 111° F. (43.8° C.)                  | Davy.                              |
| Guinea fowl,           | 110                                 | "                                  |
| Thrush,                | 109                                 | "                                  |
| Sparrow,               | 108                                 | "                                  |
| Goose,                 | 107                                 | "                                  |
| Screech owl,           | 106                                 | "                                  |
| <i>Mammalia</i> —      |                                     |                                    |
| Hog,                   | 105 (40.3° C.)                      | "                                  |
| Manatee,               | 104 abdomen,                        | Martine.                           |
| Rabbit,                | 104 to 100,                         | Prevost and Dumas,<br>de la Roche. |
| Sheep,                 | 104                                 | Davy.                              |
| Goat,                  | 104                                 | "                                  |
| Rat,                   | 102                                 | "                                  |
| Squirrel,              | 102                                 | "                                  |
| Cat,                   | 102                                 | "                                  |
| Panther,               | 102                                 | "                                  |
| Dog,                   | 102                                 | "                                  |
| Monkey,                | 101                                 | "                                  |
| Porpoise,              | 100 liver,                          | "                                  |
| Ox,                    | 100                                 | "                                  |
| Elephant,              | 99.5                                | "                                  |
| Horse,                 | 99.5                                | "                                  |
| <i>Reptilia</i> —      |                                     |                                    |
| Green snake,           | 88.5                                | "                                  |
| Tortoise,              | 87 œsophagus,                       | "                                  |
| Iguana,                | 82.5                                | "                                  |
| Alligator,             | 69                                  | Jones.                             |
| <i>Amphibia</i> —      |                                     |                                    |
| Frog,                  | 64                                  | Davy.                              |
| <i>Pisces</i> —        |                                     |                                    |
| Trout,                 | 58                                  | "                                  |
| Eel,                   | 51                                  | "                                  |
| <i>Articulata</i> —    |                                     |                                    |
| Beetle,                | 77 surrounding air 76°,             | "                                  |
| Cockroach,             | 75 " " 74°,                         | "                                  |
| <i>Mollusca</i> —      |                                     |                                    |
| Oyster,                | Temp. same as sea, 82°.             | "                                  |
| Snail,                 | 76.5 surrounding air, 76.25, °      | "                                  |
| <i>Echinodermata</i> — |                                     |                                    |
| Star fish,             | 6–10° F. above temp. of sea (66.3°) | Valentin.                          |
| Sea urchin,            | 5–10 " " " (66.7 )                  | "                                  |
| Sea cucumber,          | 6–10 " " " (67.6 )                  | "                                  |
| <i>Vermes</i> —        |                                     |                                    |
| Leech,                 | 1 " " of air (56. )                 | Hunter.                            |
| <i>Cœlenterata</i> —   |                                     |                                    |
| Anemone,               | 5–10 " " of sea (69.4 )             | Valentin.                          |
| Jelly fish,            | 7–10 " " " (72.5 )                  | "                                  |
| <i>Ponifera</i> —      |                                     |                                    |
| Sponge,                | Same as sea (68.3° F.)              | "                                  |

Of all animals, birds have the highest temperature, that of the chicken, for example, according to Davy<sup>1</sup> being as high as 111° F., (43° C.), a slightly higher temperature, according to Pallas,<sup>2</sup> even being found in certain small birds. Among mammals the temperature of the rabbit is noteworthy, amounting to 40° C. (105.8° F.). On the other hand the temperature of fishes, with some exceptions, is not usually more than 0.5° C. (0.9° F.) higher than that of the water in which they live, whilst among the invertebrata,<sup>3</sup> as in the case of mollusks, star fish, jelly fish, anemone, the excess of the temperature over that of the surrounding medium may be even less, amounting often to no more than 0.2° C. As an exception to the last statement and interesting in this connection may be mentioned the considerable amount of heat developed by bees and ants when swarming. Although a great number of observations have been made, some difference of opinion still prevails as to what constitutes the average normal temperature in man. This, however, is readily understood when, as we shall presently see, the temperature of the body not only varies considerably in different situations, but according to numerous circumstances; among others may be here very appropriately mentioned especially the manner in which the thermometrical observations should be made. It is of the highest importance, not only that the part of the body selected for taking the temperature should be mentioned, but that the thermometer used in making the observation should be a standard one.

The exact date of the invention of the thermometer as well as of that of the microscope is not exactly known, and in both instances there is also doubt as to whom the merit of these inventions should be accorded. At the present moment, for example, the invention of the thermometer is attributed on the one hand by Rosenthal<sup>4</sup> to Galileo, and on the other by Wunderlich<sup>5</sup> to Sanctorius. It is probable that it was invented by Galileo (1603), but first made use of in the study of the temperature of man in fever by Sanctorius (1626). While it is true that Galileo is mentioned in the preface to his works,<sup>6</sup> and is referred to by his biographer Viviani,<sup>7</sup> as the inventor, nevertheless, that Sanctorius considered himself as the inventor, there can be no doubt; since he himself distinctly says so,<sup>8</sup> and it may be mentioned in this connection that this claim is admitted without reserve by both Borelli<sup>9</sup> and Malpighi.<sup>10</sup> Other claims, however, like those in favor of Galileo, of a posthumous character, have been advanced by Boerhaave,<sup>11</sup> who attributed the invention to his countryman Drebbel, and by Fulgentius<sup>12</sup> to his compatriot, the great Venetian Father Paul Sarpi.

The metastatic thermometer of Walferdin (Fig. 255), is very useful since by means of it a variation of the  $\frac{1}{100}$ th of a degree Cent. (corre-

<sup>1</sup> Researches, Phys. and Anat., p. 186. London, 1839.

<sup>2</sup> Gavarret, De la Chaleur Produite par les Etres Vivants, p. 94. Paris, 1855.

<sup>3</sup> Milne Edwards: Physiologie, tome neuvieme, 1863, p. 13.

<sup>4</sup> Hermann: Handbuch der Physiologie, Vierter Band, Zweiter Theil, S. 294

<sup>5</sup> Das Verhalten der Eigenwärme in Krankheiten, 2 Aufl. 1870, S. 34.

<sup>6</sup> Opere di Galilei, p. 47.

<sup>7</sup> Vita de l'Galilei, p. 67.

<sup>8</sup> Com. in Galen, Art. Med., p. 736. Com. in Avicenna, i. p. 22, 78, 219.

<sup>9</sup> De Motu Animal, 11 Prop. 175.

<sup>10</sup> Opera Posth., p. 30.

<sup>11</sup> Elementa Chemiæ, p. 152, 156. Lugd. Bat., 1732.

<sup>12</sup> Opere del Padre, Vita del Padre, p. 158. Paola, 1687.



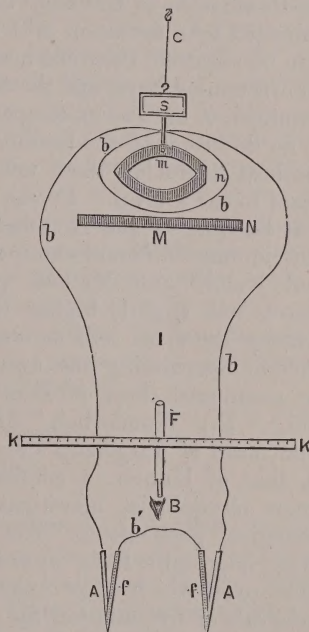
FIG. 255

Walferdin's  
metastatic  
thermometer.

sponding to a millimetre in length of the mercury) can be accurately determined, and that however excellent the instrument may be at the time obtained, it should be constantly tested. Further, in using the thermometer it should be so applied that the part whose temperature is to be determined completely surrounds the bulb of the instrument, hence, of all parts of the body, the rectum is that which is best adapted for thermometrical observations, the instrument being inserted to a depth of at least 5 cm. (2 in). On account, however, of being more convenient, the axilla is frequently made use of in determining the temperature of the human body. It must be remembered in that case then that the temperature is usually  $\frac{5}{10}$ th to 1 degree lower than that of the rectum. The tongue and vagina are also frequently made use of in taking the temperature. Apart from individual idiosyncrasies, to neglect of the precautions just referred to is undoubtedly due much of the difference of opinion that has prevailed more particularly among the older physiologists with reference to the temperature of man. If, from the nature of the case, on account of the size of the cavity to be examined, etc., the application of a thermometer is inadmissible, thermo-electric needles are then made use of in determining the temperature. Even greater precautions must be taken than when the

observation is made in the usual way on account of the delicacy of the apparatus, as slight a variation as the  $\frac{1}{4000}$ th of a degree having been determined by such. Thermo-electric needles (Fig. 256, A f, f A) are usually made of iron and German silver, each needle consisting of iron (f) and silver (A), soldered together at and near their points, and the two so disposed as to constitute together an element. The iron wires being in the middle, and the silver ones externally, if the latter are connected with each other through a galvanometer (M), a circuit is formed. The deviation of the needle will then indicate the temperature of the

FIG. 256.



Thermo-electric needles.

part examined through the electricity developed by the contact of the needles with the heated surface. The wires are, of course, except where soldered together, carefully isolated, and where held, are covered with silk and varnish. When the difference in the temperature of two parts of the body is to be determined, the two needles are imbedded in the parts, and the intensity of the current measured and the amount of heat determined, the relation between the deviation of the needle and the amount of heat producing it having been previously experimentally determined. This can be accomplished by immersing the needles with delicate thermometers attached, in oil baths differing in temperature, for example, by one degree C. The deviation of the galvanometer needle will then indicate a difference in temperature of one degree C. Suppose, further, that as measured by the scale the deviation of the galvanometer needle amounts to 150 mm., then  $\frac{1}{150}$ th of a degree C. of temperature is indicated by a deviation of 1 mm. of the needle. If absolute temperature be required, then one needle is applied to a surface maintained at a known temperature, and the other to that whose temperature is to be determined, or the known temperature can be gradually reduced until there is no deviation of the needle. The opposite currents being then equal the heat producing them must be equal—that is, the unknown heat is equal to the known. It was by means of the thermo-electric apparatus that Becquerel,<sup>1</sup> and Breschet determined the temperature of the biceps muscle under different external conditions to be referred to in a moment, and Nobili<sup>2</sup> and Melloni proved that the internal temperature of insects was slightly higher than that of the surrounding atmosphere. Among the most reliable observations that have been made with reference to determining the average temperature of the human body may be mentioned those of Hunter,<sup>3</sup> 37.2° C. (98.9° F.), Davy,<sup>4</sup> 37.3° C. (99.1° F.), Wunderlich,<sup>5</sup> 37° C. (98.6° F.), Jurgensen,<sup>6</sup> 37.2° C. The mean of Jurgensen's observations, it will be observed, is the same as that of Hunter, a confirmation of the accuracy with which that great physiologist investigated the subject of animal heat as all other biological phenomena. The results of Jurgensen's experiments are most important, both on account of their number and the length of time over which they extended. They consisted in reading off at intervals of five minutes the indications of a thermometer permanently retained in the rectum, and extended over three days. The mean obtained by Jurgensen was 37.2° C. (98.9° F.), which we will consider as being the average normal temperature of the human body, although variations between 37° and 38° C. (98.6° and 100.4° F.) may occur within the limits of health.

Among the various conditions that modify the normal temperature may be mentioned, in addition to the influence of the part of the body examined, to which we have already incidentally alluded, that exerted by age, sex, the time of day, food, muscular and mental work,

<sup>1</sup> Ann. des Sciences Naturelles, 2d ser., 1835, t. iii. p. 269.

<sup>2</sup> Ann. de Chimie et de Physique, 1831, t. xlviii. p. 208.

<sup>3</sup> Works of John Hunter, ed. by J. F. Palmer, vol. i. p. 289. London, 1835. Phil. Trans., 1844, p. 61.

<sup>4</sup> Researches, Phys. and Anat., 1839, vol. i. p. 162.

<sup>5</sup> Op. cit., S. 92.

<sup>6</sup> Deutsche Archiv klin. Med., Band iii. S. 166.



external temperature, etc. To the consideration of these let us now turn.

### AGE AND SEX.

According to Andral,<sup>1</sup> Bärensprung,<sup>2</sup> and others, the temperature before birth, as well as immediately afterward, is slightly higher than that of the mother; but as the newborn child possesses but little power of resisting external cold, its temperature soon falls, within two hours, perhaps, from  $37.8^{\circ}$  to  $35.2^{\circ}$  C. ( $100.04^{\circ}$  to  $95.2^{\circ}$  F.). Hence the importance of providing for the infant sufficient warmth by suitable means, and to the neglect of which the death in many instances is undoubtedly due. Immediately after birth the temperature of the infant taken in the rectum is between  $37.5^{\circ}$  and  $37.8^{\circ}$  C. ( $99.5^{\circ}$  and  $100.04^{\circ}$  F.), falling after the first bath to  $37^{\circ}$  C. ( $98.6^{\circ}$  F.) and even lower, while during the next ten days it varies between  $37.25^{\circ}$  and  $37.6^{\circ}$  C. ( $98.9^{\circ}$  and  $99.6^{\circ}$  F.), being notably increased by screaming, etc. During the period intervening between early infancy and the age of puberty the temperature falls about  $0.2^{\circ}$  C. ( $3.6^{\circ}$  F.), and from there on till adult life falls about  $0.2^{\circ}$  C. still more, the normal temperature or  $37.2^{\circ}$  C. ( $98.9^{\circ}$  F.) being then reached. After sixty years of age the temperature begins to rise again, and at eighty years has again reached that of the newborn child. This rise in temperature in old age is probably due to the diminished circulation of the anæmic skin, since it cannot be supposed that the production of heat has been increased. As a general rule, sex has no appreciable influence upon the temperature of the body. According to Ogle,<sup>3</sup> however, the temperature of the female appears to be slightly higher than that of the male.

### DAILY VARIATIONS.

The temperature of the body, like the frequency of the pulse, respiration, and exhalation of carbonic acid, exhibits periodical variations. From the numerous observations of Davy, Hallmann, Gierse, Bärensprung, Lichteufels, Frohlich, Damrosch, Ogle, Liebermeister, Jürgensen,<sup>4</sup> it appears that the temperature of the body increases very quickly from 6 A.M. to 11 A.M., but from that time forward increases more slowly, reaching a maximum between 5 and 6 P.M. About 7 in the evening the temperature begins to fall, reaching the minimum about 5 A.M., the difference being in 24 hours usually about  $1^{\circ}$  C. ( $1.8^{\circ}$  F.), though it may amount to as much as  $2^{\circ}$  C. ( $3.6^{\circ}$  F.).

Climate seems to influence the time of day at which the maximum and minimum temperatures occur, the minimum being reached, according to Davy, in England by midnight, but in the tropics not before 6 or 7 A.M.

<sup>1</sup> Compt. Rend., t. lxx. p. 825.

<sup>2</sup> V. Bärensprung, Arch. f. Anat. u. Phys., 1851, S. 138.

<sup>3</sup> Kirke's Physiology, 10th ed., p. 255. Phila., 1881.

<sup>4</sup> Rosenthal die Physiologie der thierischen Wärme in Hermann, op. cit., Vierter Band, S. 322.

TABLE LXV.<sup>1</sup>

| Hour.   | Barensprung. | Davy.  | Jurgensen. |       |
|---------|--------------|--------|------------|-------|
|         | Cent.        |        |            |       |
| 5       | .....        | .....  | 36.7       | 36.6  |
| 6       | 36.68        | .....  | 36.7       | 36.4  |
| 7       | .....        | 36.94* | 36.7*      | 36.5* |
| A. M. 8 | 37.16*       | .....  | 36.8       | 36.7  |
| 9       | .....        | 36.89  | 36.9       | 36.8  |
| 10      | 37.26        | .....  | 37.0       | 37.0  |
| 11      | .....        | 36.89  | 37.2       | 37.2  |
| M. 12   | 36.87        | .....  | 37.3*      | 37.3* |
| 1       | 36.83        | .....  | 37.3       | 37.3  |
| 2       | .....        | 37.05  | 37.4       | 37.4  |
| 3       | 37.15*       | .....  | 37.4*      | 37.3* |
| 4       | .....        | 37.17  | 37.5       | 37.5  |
| 5       | 37.48        | 37.05* | 37.5       | 37.5  |
| 6       | .....        | 36.83  | 37.5       | 37.6  |
| 7       | 37.43        | 36.50* | 37.5*      | 37.6* |
| P. M. 8 | .....        | .....  | 37.4       | 37.7  |
| 9       | 37.02*       | .....  | 37.4       | 37.5  |
| 10      | .....        | .....  | 37.3       | 37.4  |
| 11      | 36.85        | 36.72  | 37.2       | 37.1  |
| 12      | .....        | .....  | 37.1       | 37.4  |
| 1       | 36.85        | 36.44  | 37.0       | 36.9  |
| 2       | .....        | .....  | 36.9       | 36.7  |
| 3       | .....        | .....  | 36.8       | 36.7  |
| 4       | .....        | .....  | 36.7       | 36.7  |

Asterisk signifies that food was taken.

Supposing with Jurgensen, Table LXV., that the day temperature begins at 6 A.M. with 36.4° C., and ends at 8 P.M. with 37.7°, the duration of the former with a usually mean temperature of 37.3°, exceeds the latter with a mean of 36.9° by four hours, the average temperature for the whole day being, as already mentioned, about 37.2° C. (98.9° F.). As might be expected, Debczynski<sup>2</sup> finds that persistent night work reverses the rhythm of the variations of temperature, the thermometer standing highest in the morning (37.8°), instead of in the evening, (35.3°).

### FOOD.

As in the long run the heat, as we shall see, is due to the combustion of substances taken into the body as food, it follows that the production of heat is intimately associated with that of nutrition. Inasmuch, however, as it is not until the last stage of inanition in the starving man or animal that the temperature notably falls, it having been previously maintained in the absence of food through the combustion of the tissues, it is not to be expected that in health the mere taking of food will influence the temperature to any great extent, since the fuel, so to speak, is ordinarily consumed as rapidly as supplied, and when deficient is made up at the expense of the tissues. For example, very hot drinks increase the temperature but little. Suppose, for example, a man weighing 60 kilo. (132 lbs.) drinks a kilo. (2.2 lbs.) at 50° C. (122° F.), the temperature of the whole body (supposing it to be 37.2° C.

<sup>1</sup> Landois, op. cit., S. 406.

<sup>2</sup> Virchow u. Hirsch : Jahresber., 1875, Band i. S. 248.



and having the same specific heat as water) would be increased only about 0.2 of a degree C. It must be remembered in this instance, as in many others, that the effect of taking a hot drink is not so simple as may at first appear, since the circulation being increased by it the loss of heat through evaporation will be increased. The one effect neutralizing to a certain extent the other, the full effect of the drink as regards elevation of the temperature is not therefore experienced. Even if the drinks contain specific substances such as tea, coffee, alcohol, etc., the temperature of the body is diminished only two or three tenths of a degree C. It is possible that the loss of heat experienced in the taking of alcohol is not only due to the quickened circulation, but to a paralyzing effect exerted upon the vasomotor nerves of the skin, whereby a greater quantity of blood being conveyed to the surface than usual, more heat is consequently given off and so lost. On the other hand, while the effect of cold drinks, etc., is to diminish the temperature of the body, the diminution is also very slight, amounting usually to but a few tenths of a degree C. Thus, according to Lichteufels and Frolich, Winternitz, and others,<sup>1</sup> drinks at a temperature of 18°, 16.3°, and 4.6° C., reduced that of the body in the first two instances within 6 minutes after taking them 0.1°, 0.4°, and in the last in 70 minutes 1.4° C. Further, as in the digestion of solid foods heat is required to assist the chemico-physical changes, it might be expected that as part of the heat becomes latent the temperature of the body would be slightly diminished temporarily after taking the food, even though the temperature should be increased later through further oxidation. That such is the case seems to be shown by the experiments of Vintschgau and Dietl,<sup>2</sup> made upon a dog with gastric fistula, in which the temperature of the food introduced, and which differed but little from that of the body, first fell and then rose. From what has just been said, however, of the compensating power exercised by the economy whether food be taken or withheld, it would be inferred that the influence exerted by the taking of food upon the daily variations must be very slight, if any. Indeed, the variations in temperature that are observed after meals, as a matter of fact, occur whether food be taken or not. The most, indeed, that can be said is that if a meal be taken late in the day the diminution in temperature, characteristic of that period, is somewhat put off. Indeed, it is not until shortly before death caused by inanition or starvation, for the reasons already given, that the temperature is notably diminished.

#### MUSCULAR AND MENTAL AND GLANDULAR ACTION.

We shall soon see, in our study of muscular action, that at the moment of muscular contraction a considerable amount of heat is set free—indeed, probably three-fourths of the heat developed is produced in the muscles. Thus, according to Davy,<sup>3</sup> the temperature of the room being 66° F., that of the feet 66°, under the tongue 98°, and of the urine 100°; after a walk in the open air at 40° the temperature of the feet was 96.5° and

<sup>1</sup> Rosenthal, *op. cit.*, S. 325.

<sup>2</sup> Sitz. d. Wiener Acad. Math-Natur u. Cl. 2 Abth, lx, S. 697, 1870.

<sup>3</sup> Phil. Trans., 1844, p. 63.

the urine  $101^{\circ}$ , that under the tongue being unchanged. Indeed, daily observation as well as special experiments teaches us that our whole body is warmed by muscular exercise. Further consideration, however, will show that the body is not as much heated as one would be led to expect from the amount of heat developed under the circumstances, and from the rapidity with which the temperature of the body falls to the normal with the cessation of the exercise, it is evident that as fast as the heat is developed it is as rapidly radiated away or lost as some other mode of force. The influence of muscular exercise in elevating the temperature of the body is also well seen under certain pathological conditions; the temperature in tetanus, for example, rising, according to Wunderlich, as high as  $44.75^{\circ}$  C. ( $112.5^{\circ}$  F.). It should be mentioned, however, that this great rise in temperature can hardly be attributed entirely to muscular action, since in all probability at the same time other influences come into play, such as the acting of the vasomotor nerves, which in constricting the vessels of the skin will diminish the usual loss of heat due to radiation and evaporation.

Nervous-like muscular activity is also accompanied with the production of heat. Thus, according to Davy,<sup>2</sup> in England, during the reading of a work demanding attention the temperature of the body was increased  $0.5^{\circ}$  F. Mental effort in the tropics is accompanied by a still greater production of heat, amounting, in some instances, to more than  $2^{\circ}$  F., as in the giving of a lecture, for example; in the latter case some of the heat was probably due to the muscular action involved. Lombard<sup>3</sup> has also determined, by means of delicate thermo-electric apparatus, local increase of temperature in the head resulting from mental effort. Schiff<sup>4</sup> has also shown that the action of the nerves, as well as that of the brain, is accompanied with the production of heat. In all instances, however, the amount of heat produced, at least that appearing as such, is a small part of the heat produced, as in the case of muscle being converted, as we shall see hereafter, into other modes of force.

Glandular action is also accompanied with the production of heat due to the chemical activity incidental to secretion. Thus, according to Ludwig and Spiess,<sup>5</sup> the temperature of the saliva secreted during stimulation of the chorda tympani is 1 to  $1.5^{\circ}$  C. higher than that of the blood of the carotid artery of the same side. We have already called attention to the fact of the temperature of the blood of the hepatic vein being higher than that of any other part of the body, due, in part at least, to the size and constant activity of the liver.

### SURROUNDING TEMPERATURE.

Any consideration as to the temperature of man or animal would naturally suggest the influence exerted by that of the surrounding atmosphere, and concerning which there was, during the last century, difference of opinion. So distinguished a teacher as Boerhaave, for example,

<sup>1</sup> Op. cit., S. 400.

<sup>3</sup> Experimental Researches on the Regional Temperature of the Head.

<sup>4</sup> Archiv de phys. normal et path., 1870, pp. 5, 198, 323, 421.

<sup>2</sup> Phil. Trans., 1845, p. 443.

London, 1879.

<sup>5</sup> Wien. Sitzb., Bd. 25, 1857.



observing<sup>1</sup> that no body can endure an air heated to 90° F., and that we are always warmer than the surrounding air, supported this view by experiments performed at his request,<sup>2</sup> by Fahrenheit and Provost, which consisted in placing a sparrow, a cat, and a dog in a sugar-baker's oven, heated to 146° F., and in which it was found they soon died. Notwithstanding the result of these experiments, the great Haller, basing his opinion upon the testimony of Lining Adamson, and other travellers, as to the intense heat that prevailed in certain parts of this country, South Carolina, Senegal, and elsewhere, held<sup>3</sup> in opposition to the view entertained by Boerhaave that man could not only live in an atmosphere 16°, but even 28° F., higher than that of the blood. About this time important observations bearing upon this question were made by Franklin and Governor Ellis. In a letter dated London, June 17, 1758, in referring to a hot Sunday passed in Philadelphia, in June, 1750, Franklin<sup>4</sup> recalls that, during the day, when the thermometer was at 100° F., in the shade, his body never grew so hot as the air surrounding it, or the inanimate bodies immersed in the same air, and, with his usual acuteness, accounts for the body being kept cool under such circumstances by continual sweating, and by the evaporation of that sweat.

Within a month of the same year—that is, in July 17, 1758—Governor Ellis, in a letter to his brother in London, called attention particularly to the fact that, while in Georgia, a thermometer suspended from under an umbrella which he carried during a walk of one hundred yards registered 105° F., the temperature of his body was only 97°. The letter of Governor Ellis being communicated to the Royal Society<sup>5</sup> was thereby at once insured a wide circulation; that of Franklin, though written first, was not made public, however, till afterward.<sup>6</sup> Shortly after the observation of Ellis, just referred to, it was ascertained by Tillet,<sup>7</sup> in experimenting with a baker's oven, that the young women in attendance were accustomed to remain in it for a few minutes even when at a temperature of 260° F. (126.6° C.). In one instance Tillet, anxious for the safety of the woman, requested her to come out, but she assured him she felt no inconvenience, and remained in the oven for ten minutes, the latter having a temperature of 280° F. (160° C.), indeed, on her coming out, beyond the flushing of the face, there was nothing especially noticeable. While the facts just referred to excited considerable interest at the time, it was not till some years later, however, that any further experiments were performed with the object of ascertaining the effect of heated air upon the temperature of the body. In 1774, the subject, however, was taken up again by Fordyce, who, together with Blagden, Solander, Banks, and others, experimented upon themselves, either in a room heated with flues, and upon the floor of which boiling water was poured, or in rooms heated

<sup>1</sup> *Elementa Chemiæ*, p. 192. Lugd. Bat., MDCCXXXII.

<sup>2</sup> *Idem opus*, p. 275.

<sup>3</sup> *Elementa Physiologiæ*, p. 37. Lausanne, MDCCCLX.

<sup>4</sup> *Works*, vol. iii, p. 301. Phila., 1809.

<sup>5</sup> *Journal de Physique*, 1773, tome ii, p. 453.

<sup>6</sup> *Mem. de l'Acad. des Sciences*, 1764, tome lxxxi, p. 188.

<sup>7</sup> *Phil. Trans.*, 1759, vol. i, p. 755, Part ii.

with flues only. The result of these experiments, as described by Blagden,<sup>1</sup> may be summed up as follows :

In the room containing vapor Fordyce was able to bear for 10 minutes a temperature of  $110^{\circ}$  F. ( $43.3^{\circ}$  C.), 20 minutes  $120^{\circ}$  F. ( $48.8^{\circ}$  C.), and for 15 minutes a heat gradually increasing from  $119^{\circ}$  to  $130^{\circ}$  F. ( $48.3^{\circ}$  to  $54^{\circ}$  C.). In these experiments, it is said, that the temperature under the tongue and of the urine did not rise higher than  $100^{\circ}$  F. ( $37.7^{\circ}$  C.). In the room heated with flues only, and containing dry air, Fordyce, together with Blagden and Banks in the room, could stand, however, a higher heat than in the former instance, supporting for ten minutes a temperature of  $198^{\circ}$  F. ( $92^{\circ}$  C.). Shortly after these experiments it was ascertained by Dobson,<sup>2</sup> from observations made in the sweating-room of the Liverpool Hospital, that individuals could stand for periods between 10 and 20 minutes a temperature, if the air be dry, of between  $202^{\circ}$  and  $224^{\circ}$  F. ( $94.4^{\circ}$  and  $106.6^{\circ}$  C.). Fordyce, himself, as mentioned in a subsequent paper by Blagden,<sup>3</sup> was able to endure for 8 minutes even as high a temperature as  $260^{\circ}$  F. ( $127^{\circ}$  C.), the uncomfortable feelings experienced quickly passing away with the breaking out of a profuse sweat. The immunity possessed by persons habitually exposed from time to time to a dry atmosphere, having a temperature even higher than that to which Fordyce, Blagden, etc., were subjected, is undoubtedly due, in a great measure at least, as Franklin supposed, to the cold produced through the evaporation of the cutaneous perspiration and pulmonary exhalation. In this way can be explained how the workmen of the sculptor Chantry went into a furnace having a temperature of  $340^{\circ}$  F. ( $182^{\circ}$  C.), and Chabert, the fire king, into one at between  $400^{\circ}$  and  $600^{\circ}$  F. ( $226^{\circ}$  and  $315.5^{\circ}$  C.). Indeed, the salutary effect, under such circumstances, of keeping the temperature down by evaporation was fully recognized by Fordyce and Blagden,<sup>4</sup> and proved by them in the following way : Two similar earthen vessels, one containing water only and the other an equal quantity of water, with a bit of wax, were put upon a piece of wood in the heated room. In an hour and a half the pure water was heated to  $140^{\circ}$  F., while that containing the wax had acquired a temperature of  $152^{\circ}$  F., as the wax in melting had formed a film upon the surface of the water, and thereby had prevented evaporation. Further, it was observed that the pure water never came near the boiling-point, but if a small quantity of oil was dropped into it, as had been done before with the wax, finally the water in both vessels boiled briskly. The effect of sweating in keeping down the bodily temperature is daily seen in the taking of Turkish as compared with Russian baths, an equally high temperature being much better borne in the former, on account of the air being dry, than in the latter, where the air is moist. The profuse perspiration induced through hot baths has long been a matter of comment ; as early as the first half of the last century Le Monnier,<sup>5</sup> in speaking of the natural hot baths at Baregas, with a temperature in the hottest part of  $112^{\circ}$  F. ( $44.4^{\circ}$  C.), observes that the sweat poured

<sup>1</sup> Phil. Trans., vol. lxx., 1775, Part i. p. 111.

<sup>2</sup> Idem, p. 463.

<sup>3</sup> Idem, p. 484.

<sup>4</sup> Op. cit., p. 491.

<sup>5</sup> Mem. de l'Acad. des Sciences, 1747, tome lxxv. p. 271.



down from his face after remaining in it 8 minutes, and that after that time he was obliged to leave the bath, with reddened and swollen skin, and greatly increased pulse through violent attacks of vertigo. The conclusion drawn from the different experiments of Fahrenheit and Provost, Tillot, Fordyce, and Blagden, etc., that we have just described, was that man could not only exist in an atmosphere having a higher temperature than that of his own body, but that the latter remained unchanged, even when that of the surrounding atmosphere was greatly increased, notwithstanding that in an experiment with a dog the temperature was found by Fordyce to increase. It would appear, however, without doubt, from later observations, that with an increase in the temperature of the surrounding air there is an increase in that of the body. Thus, in the experiments made by De la Roche<sup>1</sup> and Berger, it was found that, after remaining 15 minutes in a vapor bath, with a temperature varying between 37.5° and 48.8° C. (99.5° and 119.6° F.), the temperature in the mouth was increased 3.1° C. (5.5° F.), while in dry air, but at a temperature of 80° C. (174° F.), the temperature was increased about 5° C. (9° F.). According to Davy,<sup>2</sup> also, who made a great number of observations in different parts of the world, the mean temperature of the body in the tropics is about 1° F. higher than in England. Such a variation has been held by Boileau,<sup>3</sup> for example, as abnormal, and as an indication of a slight disturbance in the system due to change of climate, and to which certain delicate persons are liable. The observations of Eydoux<sup>4</sup> and Souleyet, made during the voyage of the "Bonite," and of Brown-Séquard,<sup>5</sup> to the Isle of France, though less in number than those of Davy, so far as they go, confirm the result obtained by that reliable observer. Davy<sup>6</sup> also showed, from a number of observations, that the mean temperature of the air being 60° F. (15.5° C.), that of the body was 98.28° F. (36.7 C.), whereas, if the temperature of the air rose to 80° F. (26.6° C.), the temperature of the body rose to 99.67° F. (37.5° C.).

The temperature of individual portions of the body has been shown to increase with that of the surrounding medium, as well as that of the whole body. In an experiment of Becquerel and Breschet,<sup>7</sup> for example, where the biceps muscle was surrounded for 15 minutes by water at a temperature of 42° (109° F.), the temperature, as determined by their thermo-electric apparatus was increased two-tenths of a degree. The rise in temperature, through increase of heat in the surrounding atmosphere, can be well shown in animals. Thus, according to Rosenthal,<sup>8</sup> the temperature of a rabbit rose from the normal, 38° C. (104.4° F.) to 45° C. (113° F.), while the external temperature was increased from 32° to 40° C. (89.6° to 104° F.), death taking place at the latter temperature. Essentially the same result was obtained in the experiments of De la Roche and Berger with a guinea-pig. According to these observers, as well as Rosenthal, an increase in the temperature of 6° to 7° C. (10.8° to 12.6° F.) above the normal, however

<sup>1</sup> Thèses de l'école de médecine de Paris, 1806, No. 11.

<sup>2</sup> Philos. Transact., 1850, p. 437.

<sup>3</sup> Comp. Rend., 1838, tome vi, p. 456.

<sup>4</sup> Researches, Phys. and Anat., p. 163.

<sup>5</sup> Op. cit., S. 337.

Journal de physique, 1776, tome vii. p. 57.

<sup>6</sup> Lancet, 1878, p. 413.

<sup>7</sup> Journal de Physiologie, t. ii. p. 554.

<sup>8</sup> Ann. des Sciences Nat., 1838, p. 271.

brought about, is fatal to all animals. It would appear from these experiments as well as the earlier ones of Provost and Fahrenheit, that large animals bear a high temperature better than small ones, probably because, in the latter, a greater quantity of heat is produced relatively and more quickly. Thus, in the experiments of Fahrenheit, already referred to, of the three animals placed in the oven the sparrow died in 8 minutes, whereas the dog and the cat survived 28 minutes. According to De la Roche and Berger, a mouse died in 32 minutes, the temperature being increased from  $57.5^{\circ}$  to  $63.7^{\circ}$  C. ( $135^{\circ}$  to  $146.6^{\circ}$  F.), while a guinea-pig survived 1 hour and 25 minutes, the temperature rising from  $62^{\circ}$  to  $80^{\circ}$  C. ( $143.6^{\circ}$  to  $177^{\circ}$  F.); a young ass, however, though weak at the end of the experiment, successfully resisted for nearly three hours a temperature increased from  $60^{\circ}$  to  $75^{\circ}$  C. ( $140^{\circ}$  to  $167^{\circ}$  F.). In the case of man, in certain pathological conditions, as in typhoid and typhus fever, the temperature of the body may rise to  $40.5^{\circ}$  and  $41.1^{\circ}$  C. ( $105^{\circ}$  and  $106^{\circ}$  F.), and yet recovery take place. The highest temperature yet observed in man, and ending in recovery, was in a case of injury to the spine, reported by Dr. J. Teale,<sup>1</sup> in which the thermometer registered  $122^{\circ}$  F. ( $50^{\circ}$  C.). The elevation in temperature in sunstroke,  $104^{\circ}$  to  $112^{\circ}$  F. ( $40^{\circ}$  to  $44.4^{\circ}$  C.), is also very considerable; in such cases, however, the high temperature is to be attributed, in part at least, not only to the effect of exposure to the sun's heat, but also to the exercise taken incidental to the character of the occupation of those usually attacked, such as field and street laborers, soldiers, etc.

Inasmuch, as we have seen, through the free action of the skin, and with proper precautions taken as regards exercise, food, clothing, etc., man can live in an atmosphere the temperature of which is much higher than that of his body, it might naturally be supposed that through similar compensating agencies intense cold can be equally well resisted, if not better than intense heat. Such, indeed, experience proves to be the case, the temperature of the body of man, even when exposed to the intense cold of the Arctic regions, is almost the same as in the temperate ones, since the amount of heat generated absolutely is greater on account of the quantity and quality of food, and relatively so from the fact of the clothing, etc., being of such a character as to retain the heat produced. In animals the latter protective effect is provided for by their fur, wool, feathers, etc., as the case may be.

A glance at Table LXVI. will show how little the temperature of the body in Arctic animals differs from that of the animals in temperate regions, though the difference in the temperature of the former, as compared with that of the surrounding atmosphere, may amount to as much as  $76.7^{\circ}$  C. ( $138^{\circ}$  F.).

<sup>1</sup> Lancet, March 6, 1875.



TABLE LXVI.<sup>1</sup>—OBSERVATIONS OF PARRY.

| Animal.          | Temp. of animal.    | Temp. of air. | Difference. |
|------------------|---------------------|---------------|-------------|
| Arctic fox . . . | 41.5° C (106.7° F.) | —25.6° C.     | 67.1° C.    |
| “ “ . . .        | 38.5                | —20.6         | 59.1        |
| “ “ . . .        | 37.8                | —19.4         | 57.2        |
| “ “ . . .        | 38.5                | —29.4         | 67.9        |
| “ “ . . .        | 37.6                | —26.2         | 63.8        |
| “ “ . . .        | 36.6                | —23.3         | 59.9        |
| “ “ . . .        | 37.6                | —23.3         | 60.9        |
| “ “ . . .        | 40.3                | —20.3         | 70.7        |
| White hare . . . | 38.3                | —29.4         | 67.7        |
| Fox . . .        | 37.8                | —26.2         | 64.0        |
| “ . . .          | 41.1                | —35.6         | 76.7        |
| “ . . .          | 39.4                | —32.8         | 72.2        |
| “ . . .          | 38.9                | —31.7         | 70.6        |
| “ . . .          | 38.3                | —35.6         | 73.9        |
| Wolf . . .       | 40.5                | —32.8         | 73.3        |

On account of water being a better conductor, and having also a greater capacity for heat than air, the temperature of the body will fall more rapidly if exposed to cold water than to air at the same temperature; hence the great effect of cold baths in the treatment of fevers so much in vogue, particularly in Germany, in late years, and the great benefit derived from the application of ice in the treatment of sunstroke. While man and animals can resist the most intense Arctic cold by the agencies just referred to, nevertheless a far less degree of cold, if suddenly and directly applied to the body, will soon prove fatal. Thus, according to Rosenthal,<sup>2</sup> animals die if the temperature of their bodies be reduced to 24° C. (75.2° F.), and such is usually the case in man also, as shown by the clinical cases referred to by the same high authority; as well known, however, the temperature in cholera may fall as low as 18.3° C. (67° F.). There are some other conditions in addition to those already mentioned which may affect the temperature of the body. Of such are the effects exerted by race, country, labor, sea-sickness, and barometrical variations. As such influences are, however, either exceptional or temporary in their character, we will not dwell further upon them, merely mentioning that, according to the late distinguished Professor Dunglison,<sup>3</sup> the temperature of the uterus during labor may rise as high as 106° F. (41.1° C.), that of the vagina at the same time being 105° F. (40.5° C.).

<sup>1</sup> Gavarrret, op. cit., p. 101. Parry's Journal, p. 130. Philadelphia, 1821.

<sup>2</sup> Op. cit., S. 133.

<sup>3</sup> Physiology, 1856, 8th ed., vol. i. p. 602.

## CHAPTER XXXII.

### PRODUCTION OF ANIMAL HEAT.

HAVING considered the temperature of the body, and the various modifying conditions, it now remains to account for the production of this heat, and the manner in which the latter is regulated. Notwithstanding that a certain amount of heat is produced through the double decompositions and hydrations continually taking place in the economy,<sup>1</sup> there can be no doubt that, by far, the greatest amount of heat produced is due, as Lavoisier supposed, to the slow combustion continually going on within the body of the animal, caused by the absorption of oxygen, the interchanging of which with carbonic acid, etc., we have seen, constitutes the essence of respiration. The various theories as to the cause of animal heat put forward at different times before, and even after, the grand generalizations of Lavoisier<sup>2</sup> had been made known, have, therefore, for us, now only an historical interest. We, therefore, merely allude in a passing way to the views that attributed animal heat to the reaction of certain of the fluids of the body,<sup>3</sup> to an archæus vital spirit or kindred fetiches,<sup>4</sup> to fermentation,<sup>5</sup> movement of the blood in the vessels,<sup>6</sup> etc., recalling, however, the very remarkable work of Mayo,<sup>7</sup> and noting that Crawford<sup>8</sup> still maintained his view that animal heat was the latent heat of the inspired air, which, set free in the lungs, is taken up by the blood and carried thence, latent, to all parts of the body, becoming free heat again in the capillaries, even after the theory of Lavoisier had been developed. In our account of the progress in discovery by which the theory of respiration was slowly established we had occasion to refer to the great works of Lavoisier, in which, not only was the view of respiration essentially as we now understand it first distinctly enunciated, but the inference also drawn, which was later fully confirmed by experiment, that respiration was essentially the cause of animal heat. In the paper on the calcination of metals, brought before the Academy of Sciences, in 1775, Lavoisier had shown that in the decomposition of mercuric oxide by heat the principle (oxygen) so obtained supported both combustion and respiration, whereas, when the same substance was reduced by carbon the principle then obtained (carbonic acid gas) supported neither. These fundamental facts having been established, two years later Lavoisier<sup>9</sup> further showed that animals absorb oxygen and exhale carbonic acid, and during the

<sup>1</sup> D'Arsonval, *Comptes Rendus*, Aout 25th, 1879.

<sup>2</sup> *Mem. de l'Acad. des Sciences*, 1775-1789.

<sup>3</sup> Sylvius: *Disput. med.* cap. vii. 1879.

<sup>4</sup> Van Helmont: *Opera Omnia*, Anno 1707, pp. 174 and 734.

<sup>5</sup> Descartes (*Euvres*, ed de Cousin, t. iv. p. 437).

<sup>6</sup> Haller: *Elementa Physiol.*, t. ii. p. 286.

<sup>7</sup> *Tractatus de Respiratione*, 1668.

<sup>8</sup> *Experiments and Observations on Animal Heat*, London, 1788.

<sup>9</sup> *Mem. de l'Acad. des Sciences*, 1775, p. 520.



same year<sup>1</sup> formulated a view on combustion in general in which respiration was regarded as a slow process of combustion, oxygen being absorbed and carbonic acid and heat given off just as in the burning of coal. As might have been expected from the methods of investigation so characteristic of the great chemist and physiologist, Lavoisier did not long rest satisfied with the establishing of a generalization as to the nature of respiration and heat as important as that just referred to, but soon instituted a series of experiments with the view of ascertaining whether the amount of carbonic acid exhaled and heat produced by an animal in a given time was such as ought to be expected on the supposition that a certain amount of carbon had been burned in the body of the animal, the amount of carbonic acid given off and heat produced by the combustion of a similar amount of carbon outside of the body having been previously determined, and of so establishing the truth of his theory by experimental demonstration. For this purpose, in conjunction with Laplace, he invented the ice calorimeter.<sup>2</sup> This consisted essentially of three chambers, concentrically disposed, and which could be thoroughly closed above, two of the chambers opening below the stopcocks. In the innermost chamber was placed the substance whose heat was to be determined, in the middle one ice, the melting of which was the measure of the heat produced, it having been previously determined how much heat is required to melt a given quantity of ice, while in the outer chamber ice was also placed in order to shield that in the middle chamber from the external temperature. Having concluded from their experiments with the ice calorimeter that a pound of carbon, when burned, would produce heat enough to melt 95.6 pounds of ice,<sup>3</sup> Lavoisier and Laplace then placed a guinea-pig in the innermost chamber of their ice calorimeter, so modified as to permit of the free passage of a current of air, so that the respiration of the animal should not be interfered with, and found that in ten hours 402.7 grammes (6043.9 grains) of ice had been melted. But, of the heat given out during the experiment, and to the effect of which the melting of this amount of ice was due, part only evidently could have been produced by the guinea-pig, since, as Lavoisier observes, the animal must have lost heat through exposure to the surrounding cold; further, the ice would have been melted to a certain extent by the cooling of the watery vapor exhaled by the animal, while, finally, the amount of the melted water, measuring the heat produced by the animal, would have been increased by the admixture of the condensed water. Lavoisier felt himself, therefore, warranted in deducting from the 402.7 grammes of ice actually melted 61.19 grammes as representing the ice melted by the heat due to the extraneous sources just mentioned, and not actually produced by the animal during the experiment, the latter being, of course, the difference, and amounting to 341.07 grammes. But, the amount of carbon burned by the guinea-pig while in the calorimeter, as deduced from the carbonic acid exhaled, as determined by previous experiments, would have been only sufficient to

<sup>1</sup> *Ibid.*, 1777, p. 183.

<sup>2</sup> *Mem. de l'Acad. des Sciences*, 1780, p. 355.

<sup>3</sup> Or, as we would now express it, a pound of carbon when burned in the calorimeter produced 3740 calories or heat units—that is, heat enough to raise the temperature of 1 kilo of water 3740° C. or 3740 kilo of water 1° C.

have melted 326.75 grammes of ice, whereas, as we have just seen, at least 341.07 grammes must have been actually produced by the animal, it is evident that some of the heat produced by the guinea-pig must have been due to the combustion of some other substance than its carbon, as only 96-100th ( $\frac{326.75}{341.07} = 0.96$ ) of the heat could be ac-

counted for.<sup>1</sup> This fact, together with another one observed at the time, namely, that all the oxygen absorbed did not return in the carbonic acid exhaled, led Lavoisier<sup>2</sup> afterward (1785) to the conclusion that of the oxygen inspired part combined with hydrogen to form water and that the heat developed by the combustion of the hydrogen, if added to that due to the combustion of the carbon, would account for the heat produced by an animal, as in the experiment with the guinea-pig, just described, and which could not be accounted for by the combustion of the carbon alone. The final conclusion of Lavoisier as to the nature of respiration and calorification, based upon the closest reasoning, observation, and experiments, extending over many years, is best expressed in his own words:<sup>3</sup> "Respiration is only a slow combustion of carbon and hydrogen, and which resembles in every respect that which goes on in a lighted lamp or candle, and, from this point of view, animals which respire are true combustibles, which form and consume themselves. In respiration, as in combustion, it is the atmospheric air which furnishes the oxygen and caloric,<sup>4</sup> but, as in respiration, it is the substance itself of the animal; it is the blood which furnishes the combustible. If animals do not repair habitually by food that which they lose in respiration, the oil will soon give out in the lamp, and the animal would perish, as a lamp extinguishes itself through want of feeding. The proof of this identity of effects between respiration and combustion is immediately furnished by experiment. In fact, the air which has maintained respiration does not contain any longer, at its exit from the lungs, the same quantity of oxygen; it contains not only carbonic acid, but, in addition, more water than it contained before inspiration. But, as the vital air can convert itself into carbonic acid only by the addition of carbon, and into water only by the addition of hydrogen, and, as this double combination can not take place without the vital air losing a part of its specific caloric, it results that the effect of respiration is to extract from the blood a portion of carbon and hydrogen, and, to replace them, a portion of its specific heat, which, during circulation, distributes itself with the blood in all parts of the animal economy, and maintains there that constant temperature observed in all animals that breathe."

It would appear that this analogy, which exists between respiration and combustion, had not escaped the poets, or rather the philosophers

<sup>1</sup> The amount of ice actually melted was, according to Lavoisier (op. cit., p. 405), 13 oz., and that estimated from the combustion of the carbon, 10.38 oz. The numbers given in the text are those of Gavarret, op. cit., p. 174.

<sup>2</sup> Hist. de la Société Royale de Médecine, 1787, 568.

<sup>3</sup> Mem. de l'Acad. des Sciences, 1789, p. 570.

<sup>4</sup> To appreciate this passage it must be borne in mind that at the date when it was written oxygen was supposed to be composed of oxygen united with caloric, the principle of heat or fire, and that during the formation of carbonic acid through the combination of oxygen with carbon the caloric was set free.



of antiquity, of which they were the interpreters and the organs. The fire snatched from Heaven, the flame of Prometheus, is not merely an ingenious and poetical idea, it is a faithful picture of the operations of nature, at least for animals which breathe. We can only say with the ancients that the flame of life is lit at the moment that the infant breathes for the first time, and that it is only extinguished with its death. In considering relations so happily we are sometimes led to believe that, in fact, the ancients had penetrated further than we think in the sanctuary of knowledge, their fables being truly only allegories, under which they concealed the great truths of medicine and of physics.

And now, after a lapse of more than a century, the only essential criticism that we can make upon the magnificent views so poetically expressed, apart from the theory of caloric implied, is as to the part of the body where the combustion was supposed to take place, Lavoisier regarding the lungs as the seat of the combustion; whereas, we know now that it is going on in all parts of the body. But, even while holding this view, Lavoisier showed his profound appreciation of the phenomena, since he distinctly states, in a previous communication,<sup>1</sup> that possibly the carbonic acid is not produced, but only exchanged with oxygen in the lungs. However important his generalizations as to the matter of respiration and animal heat, nevertheless, dying on the scaffold a victim to the fury of the French Revolution, Lavoisier left his work unfinished. With the view of settling, if possible, some of the questions left undetermined by their great chemist, the Paris Academy offered, in 1821, a prize for the best essay on the origin of animal heat. The prize being awarded to Depretz, his essay was shortly afterward published,<sup>2</sup> that of the unsuccessful competitor, Dulong,<sup>3</sup> not, however, until several years afterward—in fact, after the death of its author. To avoid repetition, we will consider the apparatus and results of these experimenters together.

The calorimeter of Dulong and Depretz did not differ in principle essentially from the water calorimeter previously made use of, for the same purpose, by Crawford.<sup>4</sup> It consisted essentially, like the latter, of two chambers, an inner one, in which the animal within a willow cage was placed, and an outer one, containing the distilled water, the elevation of whose temperature was taken as the measure of the heat produced by the animal. In the calorimeter of Crawford, however, while the air of the inner chamber was gradually diminished, and at the end of the experiment was transferred to an eudiometer for analysis, in that of Dulong and Depretz the air in the inner chamber was continually renewed by air from a gasometer, and being transmitted from the inner chamber through a spiral tube placed within the water of the outer chamber, passed thence into a water gasometer, where it could be measured and analyzed, the air, in the mean time, as it passed through the spiral tube, giving off the heat (communicated by the animal) to the surrounding water, and so elevating its temperature. The amount

<sup>1</sup> Mem. de l'Acad. des Sciences, 1777, p. 191.

<sup>2</sup> Ann. de Chimie et de Physique, 1824, t. xxvi. p. 337.

<sup>3</sup> Ibid., 3ième serie, 1841, t. i. p. 440.

<sup>4</sup> Op. cit., p. 315.



of heat produced by the animal, as determined by the elevation of the temperature of the water, being expressed in calories, or heat units, a heat unit being the amount of heat necessary to elevate the temperature of a pound of distilled water one degree Cent. or Fahr., according to the thermometer used, or, as is more usually understood at the present day, the amount of heat necessary to elevate the temperature of one kilo. (2.2 lbs.) one degree Cent. The amount of heat produced by the animal expressed in heat units while in the calorimeter is then obtained by multiplying the weight of the water by the number of degrees by which the temperature of the water has been increased. Suppose, for example, that the water in the calorimeter weighed 20 kilo., and its temperature had been elevated as shown by the thermometers two degrees Cent., then 40 calories, or heat units, would have been produced during the experiment by the animal, the latter having neither gained nor lost heat, since, if the animal gained heat, it is evident that all of the heat produced was not given off to the water, and if it lost heat the latter was not produced during the experiment, but simply radiated away from it, as would have been the case with any heated body. In the first case, the heat retained by the animal must be added to the heat as determined by the calorimeter; and, in the second case, the heat lost by the animal must be subtracted. In making calorimetrical experiments, therefore, the temperature of the animal must be taken at the beginning and the end of the experiment. It must be also remembered, however, that the materials entering into the composition of the calorimeter, such as copper, iron, brass, etc., absorb heat, even if in less amount than the water, and this heat also expressed in heat units must be added to that absorbed by the water. This can be readily estimated, the weight of the materials and their specific heat, or capacity for heat, being known, the capacity for heat of water being taken as unity. Suppose, for simplicity, that the calorimeter is made out of copper, much like the one we shall use, and that it weighs 10 kilo.; now the specific heat of copper being 0.09 that of water, it is evident that if the 10 kilo. of copper be multiplied by 0.09, the product 0.90, or the water equivalent, when multiplied by the two degrees Cent. equals 1.8, which will be the amount of heat expressed in heat units absorbed by the copper, and which must be added to the 40 heat units already obtained; or, what is the same thing, if the water equivalent of the copper, 0.9, be added to the 20 kilo. of water, and the result 20.9 be multiplied by 2, the quotient will be the same as before—that is, 41.8 heat units produced by the animal. In other words, each kilo. of copper, having 0.09 the capacity of heat of a kilo. of water, 10 kilo. of copper may be regarded as equivalent to 0.9 kilo. of water, which, when added to the 20 kilo. of water and multiplied by 2, or the temperature gained, gives 41.8 heat units. It is hardly necessary to add, after what has just been said, that of the other metals usually entering into the construction of the calorimeter the heat absorbed by them, as well as that retained or given off by the animal, which, as we have seen, must be added to or subtracted from the 41.8 heat units, for example, according as the animal has gained or lost heat during the experiment, is determined in exactly the same way as in the case of

the copper. As regards obtaining the water equivalent of the animal—that is, its weight multiplied by its specific heat—a difficulty presents itself, since the specific heat of the animal has not been absolutely determined. The latter is usually accepted as being 0.8,<sup>1</sup> the mean specific heat of the tissues so far determined, that of water being 1. In determining the amount of heat given off by an animal in a calorimeter there is another consideration which must not be overlooked, and which is a slight source of error even in the best constructed calorimeters. That is the slight loss of heat due to conduction and radiation from the instrument, and which cannot be entirely prevented. The loss of heat from this cause, however, can be reduced to a very small amount by proper precautions, such as surrounding the calorimeter with down, etc., as was done by Crawford, or by lowering the temperature of the water in the calorimeter some degrees below that of the surrounding atmosphere, the supposition being that the heat absorbed by the surrounding air during the first half of the experiment would be radiated back again during the latter half, and that this source of error could, therefore, be neglected, as was admitted in the experiments of Dulong and Depretz. The loss of heat due to radiation, etc., can be also determined experimentally, and can be then taken into account in the final calculation; or, by self-regulating gas-jets, heat can be supplied to restore that which is lost. Further, it is important that the heat should be thoroughly diffused through the water in the calorimeter; this can be accomplished by the stirrers, as in the apparatus of Dulong and Depretz, or by any other suitable mechanical arrangement. The great improvement in the experiments of Dulong and Depretz, however, as compared with those of their predecessors, consisted in comparing the expired air with the inspired air, and determining the amount of heat produced and carbonic acid exhaled simultaneously; whereas, in the experiments of both Lavoisier and Crawford, this was done with the same animal, but at different times. Notwithstanding the great number of experiments performed by Dulong and Depretz, and the general acceptance with which their views were received, not much importance can be attached to them at the present day on account of the following reasons: First. That the temperature of the animal within the calorimeter was assumed to remain unchanged during the experiment, although Lavoisier had distinctly called attention to the improbability of such being the case. Second. Of the amount of carbonic acid exhaled by the animal being underestimated, part of it being absorbed by the water of the gasometer into which it passes. Third. Of the amount of heat, as deduced from the carbonic acid exhaled, being also underestimated, both on account of the estimate of Lavoisier of the heat produced by the combustion of carbon and hydrogen obtained with an ice calorimeter, being accepted as the basis of comparison with the heat produced by an animal in a water calorimeter, and because the heat-producing power of the carbon and hydrogen burned even, as determined by Lavoisier, is manifestly too low as shown by the later and accurate experiments of Fabre and Silberman;<sup>2</sup> and further, that no account was taken of the

<sup>1</sup> Liebermeister: *Handbuch der Pathologie u. Therapie des Fiebers*, p. 147. Leipzig, 1875. Rosenthal: *Archiv f. Anat.*, etc., 1878, p. 215.

<sup>2</sup> *Ann. de Chimie et de Physique*, 3ième ser., t. xxxiv. p. 357; t. xxxvi. p. 51; t. xxxvii. p. 405.



heat produced by the burning of the sulphur and phosphorus in the animal economy. Fourth. That the ratio of the carbon to the hydrogen was erroneously estimated, an important source of error, since far more heat is produced by the combustion of hydrogen than by an equal weight of carbon. Fifth. From the carbon and hydrogen, to whose combustion is the heat principally due, being supposed to exist in the free condition, which they evidently do not. Sixth. From the fact, to a certain extent, of the exhalation of carbonic acid and water not being a measure of the heat produced, some heat being evolved through double decomposition and hydration, etc., without carbonic acid and water being necessarily exhaled and of carbonic acid and water being exhaled through the decomposition of the principles containing these substances, without the heat being evolved. This last objection applies to all calorimetical experiments in which the heat produced by the living body is estimated from the carbonic acid and water exhaled. It is true, that later investigators have endeavored to utilize the results of Dulong and Depretz in considering them as influenced by the conditions just referred to, since the attempts, however, have been far from satisfactory, it is not necessary for me to dwell upon them. While the results of Dulong and Depretz, even when so corrected, cannot be accepted, nevertheless the conclusion arrived at by these experimenters exercised a most important and beneficial influence upon the progress of physiology, since it was shown by them that the experimental method was the only one by which the phenomena of animal heat could be successfully studied, that so-called vital phenomena are physico-chemical phenomena, and must be investigated in exactly the same manner as the latter, a view which had fallen entirely into disrepute in France since the death of Lavoisier, the influence of Bichat being so preëminent. In the words of that otherwise profound thinker,<sup>1</sup> "let us leave to chemistry its affinity, as to physics its elasticity, its gravity—let us employ for physiology only sensibility and contractility."

To the *deus ex machina*, the vital force, that physiological fetich, then as even now every unexplained phenomenon was attributed. Indeed, it may yet be asked how long will it be before such an idea as a vital force acting as an entity is entirely banished to that obscurity where such a conception similar to that of nature abhorring a vacuum, etc., has long since been relegated. During late years a number of investigations have been made calorimetrically, with the object of determining the heat produced by an animal in a given time. Among these may be mentioned especially those of Senator<sup>2</sup> upon dogs. The calorimeter used in these experiments was essentially the same as that of Dulong's, the only difference being that it was usually filled with warm water in order to prevent the animal losing heat. The ventilation of the chamber in which the animal was placed was maintained by aspiration, the current of air, before entering the calorimeter, being freed from its carbonic acid by passing it through potash, and the carbonic acid exhaled into it by the animal being determined after it left it by Pettenkofer's method. In the final estimation of the heat produced by the animal in addition to that taken up by the calorimeter, the heat absorbed by the air passing

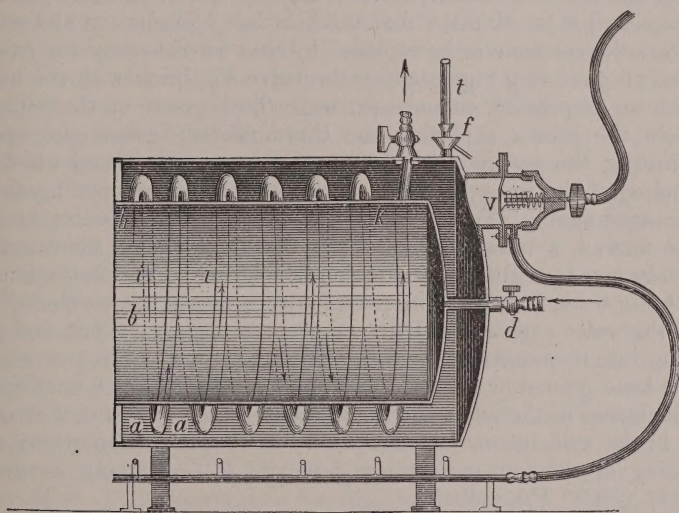
<sup>1</sup> Anatomie Générale, tome i. p. 16. Paris, 1818.

<sup>2</sup> Archiv f. Anat. u. Phys., 1872, S. 1; 1874, S. 18.

through as well as that lost through conduction and radiation, was also taken into consideration. Senator found, as the mean of his experiments, that a dog fed daily produced 16.5 calories or heat units per hour, with an exhalation during the same time of 4.4 grammes of carbonic acid, as a general rule, there being produced 2.5 calories for every kilo. (2.2 lbs.) of weight. In order to obtain the amount of heat produced in twenty-four hours, it is usual to multiply the 16.5 calories, *e. g.*, by 24, but as it is uncertain whether the production of heat is constant, this is hardly admissible. The general conclusion to be drawn from the experiments of Senator is, that there is no constant relation existing between the production of heat and the exhalation of carbonic acid, and while during digestion the production of both is increased, in starvation both are diminished.

The calorimeter (Fig. 257) that we make use of consists of two copper cylinders concentrically disposed, the outer space *a*, or the space between

FIG. 257.



Calorimeter.

the cylinders being closed at both ends with copper, the inner space *b*, or the space within the cylinder, being closed at one end by copper and at the other end by an annular door consisting of brass and glass, and which can be hermetically closed by the brass clamps and rubber facing soldered to the brass rim internally. The outer chamber *a* is filled with distilled water by means of a funnel introduced through the opening *f*, and when full contains 18.1 kilo. (40 lbs.) of water. The inner chamber *b*, at the end opposite the door, communicates by a stop-cock (*d*) with the external air, and through the opening *h* in its roof with a copper spiral, which, after making a dozen turns around the inner cylinder within the water of the outer chamber, terminates in the opening *k* of the latter. By means of the mercurial pump (already described) the ventilation of the inner chamber can be thoroughly maintained,



the air entering the latter through the opening at *d* and passing thence by the opening *h* into the spiral *i* and out by the opening *k* with the same temperature at which it entered, the heated air being gradually cooled as it passes through the spiral, the heat being absorbed by the surrounding water. If it is desired to compare the expired with the inspired air, the air freed from its water and carbonic acid by Voit's method is made to pass through a meter, before it enters the calorimeter and through one after it leaves it, being previously freed from its water and carbonic acid in the same manner as was the inspired air. Fitting in the floor of the inner chamber of the calorimeter is a movable copper pan with a sieve-like cover on which the animal rests, the object of the cover being that the urine of the animal can trickle into the pan and insure cleanliness. Ventilation having been assured by the action of the pump, and the temperature of the water in the outer chamber noted by introducing a thermometer into the opening *f* and that of the animal taken, the latter, having been previously weighed, is placed within the chamber on the tray and the door securely closed. Suppose the experiment has lasted one hour, and it be admitted that the heat lost by radiation and conduction from the calorimeter be replaced by that furnished by the gas jets, the flow of gas being regulated by the valve *V*, which with the heating of the water is pressed outward (through the pressure of the column of water in the tube *t*, replacing the thermometer) against the opening transmitting the gas and thereby diminishing its flow, and which with the cooling of the water, is drawn back again from the opening, thereby increasing it again. To determine the calories or heat units produced by the animal, a rabbit, for example, during the time mentioned, we have only now to multiply the number of degrees by which the temperature of the water has been increased by its weight, to which has been added the water equivalent of the copper, brass, glass, rubber, and solder entering into the construction of the calorimeter, and adding or subtracting the heat gained or lost by the animal as determined immediately at the conclusion of the experiment. Suppose that the temperature of the water in the calorimeter has increased  $0.5^{\circ}$  C., the temperature at the beginning of the experiment being  $15^{\circ}$  C. ( $59^{\circ}$  F.), and at the end  $15.5^{\circ}$  C. ( $59.9^{\circ}$  F.), and the

|                          |   |            |   |       |   |       |
|--------------------------|---|------------|---|-------|---|-------|
| Water equivalent, copper | = | 21 lbs.    | × | 0.095 | = | 1.995 |
| " " brass                | = | 23.25 lbs. | × | 0.093 | = | 2.162 |
| " " iron                 | = | 0.09 "     | × | 0.11  | = | 0.009 |
| " " glass                | = | 1.25 "     | × | 0.19  | = | 0.237 |
| " " rubber               | = | 0.6 "      | × | (1)   | = | 0.01  |
| " " tin                  | = | 0.5 "      | × | 0.05  | = | 0.025 |
| " " lead                 | = | 0.5 "      | × | 0.03  | = | 0.015 |
| " " materials            |   |            |   |       | = | 4.443 |

Adding the water equivalent of the materials used, 4.4 lbs., to the weight of the water, 40 lbs., making 44.4 lbs., or 20.1 kilo., and multiplying the latter by  $0.5^{\circ}$  C., the number of degrees gained by the water, the product, 10.05, will be the number of calories or heat units produced

<sup>1</sup> Specific heat of rubber slip not being determined, the heat actually produced was slightly greater than that given in text. The amount, however, would be so small that it may be neglected.

by the animal, supposing the temperature of the latter to have remained unchanged. Suppose the animal, however, lost  $0.9^{\circ}$  C., its temperature being  $39.2^{\circ}$  C. at the beginning of the experiment and  $38.3^{\circ}$  C. at the end, then there must be subtracted from the 10.05 calories 2.16—that is, the product of the weight of the rabbit, 6.6 lbs. or 3 kilo., by its specific heat,  $0.8^{\circ}$  by  $0.9^{\circ}$  ( $3 \times 0.8 \times 0.9 = 2.16$ ); the total number of heat units produced by the rabbit in the hour would then be 7.8 calories. If the rabbit gains the same number of degrees, then the 2.16 calories must be added to instead of being subtracted from the 10.05 heat units. Calorimetrical investigations have been made also upon man by Scharling,<sup>1</sup> Vogel,<sup>2</sup> and Hirn,<sup>3</sup> but with rather unsatisfactory results. The apparatus made use of by these experimenters was essentially the same, consisting of a chamber in which the man was placed and which was kept in a room maintained at a temperature as constant as possible, the increase in the temperature of the chamber, together with the heat lost through cooling, being regarded as produced by the man during the experiment. Since the temperature of the chamber after being somewhat elevated after that remains constant, the heat as produced being radiated away, according to the Newtonian law of cooling, the amount of heat produced will be equal to the difference between the constant temperature and the initial temperature multiplied by the coefficient of cooling, the latter being determined experimentally. In the experiments of Scharling and Vogel this was accomplished by placing a vessel filled with hot water in the chamber and comparing the loss of heat with the increase of the chamber, and in those of Hirn by burning hydrogen and comparing the actual result with that obtained by calculation. On account of the many sources of error incidental to such a crude method of experimentation as that just described, an approximate value only can be attached to the results so obtained, and the same may be said of the estimates of the amount of heat produced based upon the rise in the temperature of the water of a bath in which a man is immersed,<sup>4</sup> or of that of a calorimeter inclosing only a part of a person, a limb, for example.<sup>5</sup> Nevertheless, it should be mentioned that the estimates of these observers of the heat produced by a man in twenty-four hours do not differ as much as might be supposed, amounting, according to Scharling, Vogel, Hirn, Liebermann, and Leyden, to 3168, 2400, 3720, 3525, and 2376 calories respectively, allowance being made for the size and weight of the individual experimented upon.

Since the heat produced by an animal is due to the combustion of its food, it might appear at first sight that it would be only necessary to determine the amount of combustible materials, carbon, hydrogen, sulphur, phosphorus, etc., in the food, and the products of its combustion carbonic acid, water, urea, etc., in the excreta in order to determine the amount of heat produced, on the principle of the heat produced by the animal depending upon the fuel supplied and consumed, the calorimeter being used as a test of the accuracy of the results so obtained.

<sup>1</sup> Journal für pract. Chemie, xlviii. S. 435, 1849.

<sup>2</sup> Archiv d. ver. f. Wiss. Heilk. Neue folge, Band i. S. 441. 1865.

<sup>3</sup> Recherches sur l'équivalent mécanique de la chaleur, Colmar, 1858. Exposition analytique et expérimentale de la théorie mécanique de la chaleur, 3d ed., t. i. p. 27. Paris, 1875.

<sup>4</sup> Liebermeister, op. cit., p. 239.

<sup>5</sup> Leyden: Deutsch. Archiv f. klin. med., 1869, S. 273.



It must be borne in mind, however, that to effect the combustion of the food—that is, its transformation into carbonic acid, water, etc., a certain amount of heat, or an equal amount of force of some kind, is required, since the carbon, hydrogen, and other combustible matters do not exist in the food in the free gaseous state, but in a state of molecular combination. A certain unknown amount of heat would have to be deducted therefore from the amount estimated if based upon an analysis of the food and the excreta. In other words, the heat producing power of food, or any fuel, cannot be estimated from the amount of combustible matters it may contain, since the heat to be expended in breaking up the chemical combinations constituting these matters, and of setting free the heat previously locked up in them is practically unknown. It is for the reasons just given, as well as for the further one of the accepted estimates of Dulong of the amount of heat produced by the combustion of a given weight of carbon, hydrogen being too low, that the calculation of Helmholtz<sup>1</sup> of the amount of heat produced by a man weighing 82 kilo. in twenty-four hours, viz., 2731.2 calories, can only be accepted as approximating the truth. And while the calculation of Ludwig,<sup>2</sup> of a daily production on the average of 3191.9 calories is free from the last source of error mentioned, being based upon the data of Barral and the higher estimates of Fabre and Silberman of the heat value of the carbon and hydrogen burned, nevertheless, as it also assumes that the combustion of the carbon and hydrogen of the food develops as much heat as if existing in the free condition, it is open to the same objection as the calculation of Helmholtz. In fact, the only way in which the amount of heat produced through the combustion of food can be actually determined, is by burning it in a calorimeter, as was done by Frankland,<sup>3</sup> and of so obtaining its heat value by direct experimentation. The instrument we make use of for this purpose, the same as that of Frankland, of the convenient form devised by Thompson, consists of a copper cylinder with a capacity of 120 c. cm. open below, and with the rim perforated by a small opening, but closed above, and with the cavity of the cylinder prolonged into a narrow tube provided with a stopcock near its end, and of a smaller cylinder with a capacity of 15 c. cm. open above, but closed below, the lower portion of the cylinder fitting into the little cup of the stand, the latter being provided with three elastic springs which securely hold the large cylinder when the latter encloses the small one. Within the small cylinder is placed the substance to be burned with a small fuse attached with a combustible whose heat values are known. The latter being lighted, the large cylinder is immediately placed over the small one, the elastic springs holding it fast, and the instrument so put together at once plunged into a long, narrow vase containing a known quantity of distilled water whose temperature has been accurately determined by a specially constructed thermometer graduated into tenths. In a few moments fumes will be seen to issue from the holes in the rim of the outer

<sup>1</sup> Encycl. Wörterbuch der Med. Wissen, Band xxxv. S. 555 Berlin, 1846.

<sup>2</sup> Lehrbuch der Physiologie des Menschen, Zweiter Auflage, Zweite Band, S. 749. Leipzig, 1861.

<sup>3</sup> Philos. Mag., 1866, xxxii. p. 182.

cylinder into the surrounding water. The deflagration being ended, and the stopcock opened, the water will rise through the holes into the cylinders. The instrument being moved up and down, the heat given out will soon diffuse itself equally throughout the water, the amount of heat produced by the food burned being determined by the elevation of the temperature of the latter, due allowance being made on the one hand for the heat absorbed by the copper, etc., and on the other for that produced by the burning of the fuse and combustible used. The other sources of error incidental to the working of the apparatus are so slight that they may be, according to Frankland, neglected. It was by means of the calorimeter just described that Frankland determined by actual experiment the amount of heat developed by the combustion of different kinds of food. It will be seen, however, at a glance at Table LXVII., drawn up from the results obtained by this observer, that the fatty and carbohydrate foods are as thoroughly burned in the body as out of it, though more slowly, whereas the albuminous substances are but imperfectly so. This is as might have been expected, since, as we have already mentioned, except in certain temporary conditions in a state of health, fat and starch are never found in the excreta, these substances passing out of the body as carbonic acid and water, being as thoroughly oxidized within the system as if burned in pure oxygen outside of it, whereas, as we shall presently see, uric acid and urea are normal constant ingredients of the excreta, these substances representing so much unburned albumen which passes out of the system in this form.

TABLE LXVII.<sup>1</sup>—HEAT DEVELOPED BY BURNING 1 GRAMME (15.4 GR.) OF DIFFERENT ARTICLES OF FOOD EXPRESSED IN HEAT UNITS.

A heat unit is equal to the amount of heat necessary to raise the temperature of 1 kilo. (2.2 lbs.) of distilled water 1° Cent. (1.8° F.).

|                           | When oxidized outside of body. |                    | When oxidized inside of body. |                    |
|---------------------------|--------------------------------|--------------------|-------------------------------|--------------------|
|                           | Dry.                           | Natural condition. | Dry.                          | Natural condition. |
| Cod-liver oil . . . . .   | 9.069                          | 9.107              | 9.069                         | 9.107              |
| Fat of beef . . . . .     | 9.069                          | 9.069              | 9.069                         | 9.069              |
| Butter . . . . .          | 9.069                          | 9.069              | 9.069                         | 9.069              |
| Guinness' stout . . . . . | 6.401                          | 1.076              | 6.401                         | 1.076              |
| Arrowroot . . . . .       | 3.912                          | 3.912              | 3.912                         | 3.912              |
| Lump sugar . . . . .      | 3.348                          | 3.348              | 3.348                         | 3.348              |
| Grape sugar . . . . .     | 3.227                          | 3.227              | 3.227                         | 3.227              |
| Yolk of egg . . . . .     | 6.460                          | 3.423              | 6.24                          | 3.30               |
| Hard boiled egg . . . . . | 6.321                          | 2.383              | 6.05                          | 2.28               |
| Cheese . . . . .          | 6.114                          | 4.647              | 5.74                          | 4.36               |
| Mackerel . . . . .        | 6.064                          | 1.789              | 5.71                          | 1.61               |
| Lean of beef . . . . .    | 5.313                          | 1.567              | 4.85                          | 1.42               |
| Milk . . . . .            | 5.093                          | 0.662              | 5.07                          | 0.62               |
| White of egg . . . . .    | 4.896                          | 0.671              | 4.21                          | 0.57               |
| Veal . . . . .            | 4.514                          | 1.314              | 4.02                          | 1.11               |
| Ham (boiled) . . . . .    | 4.343                          | 1.980              | 3.68                          | 1.68               |
| Bread (crumb) . . . . .   | 3.984                          | 2.231              | 3.84                          | 1.45               |
| Flour . . . . .           | 3.936                          | 3.936              | 3.84                          | 3.84               |
| Rice (ground) . . . . .   | 3.813                          | 3.813              | 3.76                          | 3.76               |
| Cabbage . . . . .         | 3.776                          | 0.434              | 3.65                          | 0.42               |
| Potatoes . . . . .        | 3.752                          | 1.013              | 3.69                          | 0.99               |

<sup>1</sup> Frankland, op. cit.



According to Frankland, while 1 gramme of ox flesh and of albumen will produce, when burned out of the body, 5.103 and 4.988 heat units, the same amount of these substances when burned in the body will produce only 4.368 and 4.263 heat units respectively, the difference of 0.735 heat unit being due to that amount of heat passing out of the system latent locked up—so to speak—in the urea or the unburned albumen, 1 gramme of urea producing, when burned outside of the body, 2.206 heat units. In estimating the amount of heat produced by the burning of albumen within the body, as based upon that produced when burnt outside of it, about one-third must therefore be deducted as representing so much incombustible matter. Thus 1 gramme of albumen, when burned outside of the body, will give 4.998 heat units, of which albumen and urea constitute about one-third; deducting 0.735 heat unit, or the heat that would be produced were the urea burned in the system, there remain 4.263 heat units as the actual amount of heat produced when the albumen is burned in the system.

Having learned the amount of heat developed in the burning of a given weight of sugar, fat, albumen, etc., out of the body, it still remains, knowing by analysis how much of such substances is contained in the food, to determine from the carbonic acid, water, and urea in the excreta, or the products of the combustion of such substances, the amount actually burned in the body, and of so estimating, by means of the above data of Frankland, the amount of heat developed within the body on a normal diet, or otherwise. In other words, the ingesta or the food must be compared with the egesta or the excretions. The subject of the observation must be weighed at the beginning and the end of the experiment to learn whether the weight has remained unchanged, since, if the individual loses weight, the food has been deficient, the body wasting to supply it; and, if the reverse is the case, the food has been in excess, the body fattening. Further, the experiment should extend over a period of twenty-four hours, and longer, when possible, in order to avoid the usual source of errors incidental to all experiments of such a character if lasting for shorter periods of time. It was on such principles that the admirable experiments of Ranke, performed upon himself, were conducted, and it may be mentioned, incidentally, in this connection, that at that time the distinguished physiologist was twenty-four years old, six feet high, weighed one hundred and fifty-four pounds (70 kilos.), was in perfect health, and that the apparatus made use of was the Pettenkofer respiration apparatus that we have already referred to. The results obtained by Ranke, by means of the method just described, may be seen from Table LXVIII.

TABLE LXVIII.<sup>1</sup>—HEAT PRODUCED IN 24 HOURS BY THE COMBUSTION OF FOOD WITHIN THE BODY AS ESTIMATED FROM THE EGESTA, AND EXPRESSED IN HEAT UNITS.*Nitrogenous Diet.*

| Ingesta.            |                  | N     | C      | Egesta.      |           | N             | C      |
|---------------------|------------------|-------|--------|--------------|-----------|---------------|--------|
| Meat.               | 1832 grammes,    | 62.29 | 229.36 | Urea,        | 86.3      | 40.28         | 17.26  |
|                     | 1300 " consumed, | 44.19 | 162.75 | Uric acid,   | 1.9       | 0.65          | 0.70   |
| Fat of meat,        | 70 "             | 0.00  | 50.27  |              |           |               |        |
| Salts,              | 31 "             | ...   | ...    | Salts,       | 26.6      |               |        |
| Water,              | 3371 c.c.        | ...   | ...    | Urine,       | 2073 c.c. |               |        |
| Fat of body,        | 75.14 grammes,   | 0.00  | 54.02  | Feces,       | 99.0      | 3.26          | 14.88  |
| Water "             | 71.00 "          | ...   | ...    | Respiration, |           |               | 231.20 |
|                     |                  | 44.19 | 267.04 |              |           | 44.19         | 267.04 |
| Initial weight      |                  | .     | .      | .            | .         | 72.927 kil.   |        |
| Terminal weight     |                  | .     | .      | .            | .         | 72.781 "      |        |
|                     |                  |       |        |              |           | 0.146 gramme. |        |
| Heat units produced |                  | .     | .      | .            | .         | 2779.5        |        |

*Starvation Diet.*

| Ingesta.            |                | Egesta.      |                      |
|---------------------|----------------|--------------|----------------------|
| Body consumed.      |                | Urea,        | 18.3 grammes.        |
| Albumen,            | 54.45 grammes. | Uric acid,   | 0.24 "               |
| Fat,                | 195.94 "       | Respiration, | 180.00 cubic metres. |
| Heat units produced |                | .            | 2012.8               |

*Non-nitrogenous Diet.*

| Ingesta.            |              | Egesta.      |                      |
|---------------------|--------------|--------------|----------------------|
| Starch,             | 300 grammes. | Urea,        | 17.1                 |
| Sugar,              | 100 "        | Uric acid,   | 0.54                 |
| Fat,                | 150 "        | Feces,       | 90.00                |
| Albumen of body,    | 51.55 "      | Respiration, | 200.00 cubic metres. |
| Heat units produced |              | .            | 2059.5               |

*Mixed Diet.*

|                     |   |   |   |   |   |      |
|---------------------|---|---|---|---|---|------|
| Heat units produced | . | . | . | . | . | 2200 |
|---------------------|---|---|---|---|---|------|

It will be observed by looking at the table that the greatest amount of heat was produced on a nitrogenous, or a very abundant meat diet, but that this was accomplished at the expense of the body, Ranke losing 146 grammes in weight, his body supplying 75.14 grammes of fat in addition to the 70 grammes of roast meat and 71 grammes of water, and that of the 1832 grammes of meat eaten only 1300 grammes were burned, as shown by the amount of urea excreted. It follows, therefore, that, so far as the production of heat was concerned, the same result might have been obtained with 532 less grammes of meat, but with 71 more grammes of fat. On the other hand, as Ranke mentions in speaking of the heat produced on a non-nitrogenous diet, of the 150 grammes of fat eaten only 68.5 grammes could have been burned, 81.5 grammes having been deposited in the body. On such a diet, therefore, more than half the fat, if taken with the view of producing heat, would be superfluous. While the heat developed on a mixed diet, as may be seen from Table LXVIII., amounts, according to Ranke, to 2200

<sup>1</sup> Ranke: Physiologie Dritte Aufl., S. 196, S. 566. Leipzig, 1875.



heat units, Vierordt<sup>1</sup> estimates it at 2497, and Voit<sup>2</sup> even still higher (3066). It should be mentioned, however, that the food, at the expense of which the latter amount of heat is produced, contains far more albumen, fat, starch, sugar, etc., than that taken by Ranke<sup>3</sup> in his experiments, as may be seen from the following :

TABLE LXIX.

|                | Albumen. | Fat. | Starch or sugar. | Total.       |
|----------------|----------|------|------------------|--------------|
| Ranke . . .    | 100      | 100  | 240              | 440 grammes. |
| Vierordt . . . | 120      | 90   | 330              | 540   "      |
| Voit . . .     | 118      | 50   | 500              | 668   "      |

Let us take, however, the lowest estimate, that of Ranke, and suppose that the heat produced by the burning of the food will produce 2200 heat units—that is, an amount of heat that will elevate the temperature of 2200 kilo. of distilled water one degree Cent., that is, 70 kilo. 31.4° C., or, what is the same thing, 154 pounds of water 56.5° F.: such an amount of heat, if applied to the heating of the human body, would elevate its temperature 1.7° C., or 3° F. higher, since a human being weighing 70 kilo. (154 pounds) consists of only three-fifths water, the remaining two-fifths being tissue, and the specific heat of the latter being less (0.8) than that of the water, the same amount of heat, namely, 2200 heat units, when applied to the heating of a body weighing 70 kilo., consisting of 44.1 kilo. of water and 25.9 of tissue, must naturally elevate its temperature higher than if the 70 kilo. to be heated consisted of water alone, as shown by the following: 25.9 kilo. of tissue multiplied by its specific heat, 0.8, gives 20.7 kilo. to be added to the 44.1 kilo. of water, making 64.8 kilo. of water to be heated instead of 70 kilo.; dividing the 2200 kilo. by the former number, 64.8, the quotient, 33.1° C. (59.5° F.), is the number of degrees to which the temperature of a man weighing 70 kilo. (154 pounds) would be elevated by the burning of his food. In other words, the tissue of the human body, from this point of view, bears the same relation to its water as the brass, copper, etc., do to the water of the calorimeter, the human body, in fact, serving as a calorimeter for the determination of the heat value of foods when burned within the body. Suppose the temperature of the human body, for example, was reduced to 70° F., or lower, as is the case in cholera, it is evident on the above supposition that, upon a normal diet, the temperature would be elevated within twenty-four hours to about 131° F. On the other hand, suppose the temperature of the body was normal, the heat of the food would elevate it from 98.9° F. to nearly 160° F., and yet, as we have already seen, the temperature of the human body varies but little.

It now remains for us, in conclusion, to endeavor to account for this constant temperature somewhat more in detail than we have already done, and that leads us to the consideration of the expenditure of the heat produced.

<sup>1</sup> Physiologie Vierte Aufl. S. 257. Tub., 1871.

<sup>2</sup> Ueber die Kost in einigen öffentlichen Anstalten, 1877.

<sup>3</sup> Ranke, op. cit., p. 207.

## CHAPTER XXXIII.

### EXPENDITURE AND REGULATION OF HEAT.

WE have seen that there are produced within the human body in twenty-four hours between 2200 and 2300 calories, or heat units; that is, heat enough to raise the temperature of 2300 kilo. of water  $1^{\circ}$  C., or 23 kilo.  $100^{\circ}$  C., or, what is the same thing, about 50 pounds of water from the freezing to the boiling point. It is very evident, therefore, that were such a production of heat kept up, and the heat developed not dissipated, but retained in the body, that the latter, in the course of two days, would boil. A little reflection will show, however, that, in addition to the heat given off through radiation and conduction, if the temperature of the body be higher than that of its surroundings, that a certain amount of heat leaves the body in a latent condition, so to speak, locked up in the watery vapor exhaled from the lungs and skin, and from the fact of the solid and liquid food, and the air breathed entering the body at a lower temperature,  $15^{\circ}$  C. ( $69^{\circ}$  F.), for example, than that of the latter, and leaving it at the same temperature,  $38^{\circ}$  C. ( $100.4^{\circ}$  F.), heat must also be absorbed, and that there must be a still further expenditure of heat in the accomplishing of bodily and mental work, since there can be no doubt that, whatever be the nature of muscular and mental force, the latter is correlated in some way with heat, the disappearance of the one being coincident with the appearance of the other. Now, from the very nature of the case, the relative amounts of heat expended in the ways mentioned must vary very much, according to the character of the climate, of the quantity and quality of air breathed, of food taken, of the amount of muscular and mental work performed. It is therefore impossible, if for these reasons only, to indicate exactly what becomes of the heat developed in the body. Further, however, too much importance must not be attached to the following table, since the data upon which such a table must be based are, to a certain extent, assumed, or, as will be seen, are, indeed, entirely wanting. It is only offered as illustrating in a more detailed way the general observations regarding the expenditure of the heat just made, and as also showing the manner in which such a table could be drawn up if all the data had been without cavil experimentally determined. It should be mentioned, however, that this criticism applies only to the relative amounts of expenditure of the heat, the total amount of heat leaving the body being, of course, that produced if the temperature of the body remains constant. With these qualifications, before calling attention to Table LXX., one or two points should be mentioned in order to understand the manner in which the results so tabulated were obtained.

We will suppose that the food of a man weighing 60 kilo. (132



pounds) produces in twenty-four hours 2300 calories, or heat units; that the food of such a man, including the air breathed, be known; that the specific heat of the food be accepted as being 0.8, and that of the air 0.26; that the amount of watery vapor exhaled from the lungs and skin has been determined; that it be admitted that it requires 582 heat units to vaporize 1 kilo. of water; that the work incidental to the circulation and respiration be known, and, further, that the muscular work performed by the man during a day be considered as amounting to 112,397 kilogramme-metres, that is to say, the man does an amount of work equivalent to lifting 112,397 kilo. (247,273.4 pounds), or, 110.8 tons 1 metre (3.2 feet) high, or, what is the same thing, 354 tons through one foot, and that the amount of heat necessary to raise the temperature of one kilo. (2.2 pounds) of water  $1^{\circ}$  C. ( $1.8^{\circ}$  F.), or a heat unit, if applied mechanically, would raise 423 kilo. (930 pounds) 1 metre (3.2 feet) high, or 2977.9 pounds, or 1.4 ton, through one foot. The above being admitted, it follows that the heat produced is expended somewhat as follows:

TABLE LXX.—EXPENDITURE OF HEAT.

|                                              |   |                                      |           |                  |                |
|----------------------------------------------|---|--------------------------------------|-----------|------------------|----------------|
| 1.5 kil. ( 3.3 lbs.) water                   | . | .                                    | .         | 34.5 heat units. | 1.50 per cent. |
| 1.5 " solid food, raised 23° C (73° F.)      | . | .                                    | .         | 27.6 " "         | 1.20 " "       |
| 16.0 " (35.2 lbs.) air inspired              | . | .                                    | .         | 95.6 " "         | 4.15 " "       |
| <hr/>                                        |   |                                      |           | <hr/>            |                |
| 19.0 kil. (41.8 lbs.)                        |   |                                      |           | 157.7 " "        | 6.85 " "       |
| 0.4 kil. ( 8172 grs.) water evap. from lungs |   |                                      |           | 232.8 " "        | 10.12 " "      |
| 0.6 " (10183 grs.) " " " skin                |   |                                      |           | 384.1 " "        | 16.70 " "      |
| <hr/>                                        |   |                                      |           | <hr/>            |                |
| 1.0 kil. (18355 grs.)                        |   |                                      |           | 616.9 " "        | 26.82 " "      |
| Radiation and conduction                     | . | .                                    | .         | 1156.3 " "       | 50.27 " "      |
| Work                                         | { | circulation, 43917 kil. 138 ft. tons | 98.5 " "  | 4.28 " "         |                |
|                                              |   | respiration, 1590 " 25 "             | 17.8 " "  | 0.77 " "         |                |
|                                              |   | nervous,                             |           |                  |                |
|                                              |   | muscular, 112397 " 354 "             | 252.8 " " | 10.99 " "        |                |
| <hr/>                                        |   |                                      |           | <hr/>            |                |
|                                              |   | 157904 " 517 "                       | 369.1 " " | 16.04 " "        |                |
| Ratio of work to heat                        |   |                                      |           | .                | 1 to 6         |
| Ratio of muscular work to heat               |   |                                      |           | .                | 1 to 9         |

It will be observed from Table LXX., that of the 2300 heat units produced in twenty-four hours, about 7 per cent. are expended in warming the food, including the water and air breathed; 26 per cent. in evaporating the water from the lungs and skin; 50 per cent. in radiation and conduction from the general surface of the body, and about 16 per cent., or one-sixth of the whole heat produced in the performance of work. It must be borne in mind, however, that the 116.3 heat units, or 5.05 per cent. of the whole heat produced, and at the expense of which the work of maintaining the circulation and respiration is maintained, are only temporarily converted into mechanical energy, the latter being almost entirely reconverted into heat again, owing to the various obstructions that are offered to the movement of the blood and respiratory organs. The 5.05 per cent. heat units leaving the

body as heat, must be added, therefore, to the 50.5 per cent. expended in radiation and conduction, making the latter really amount to 55.55 per cent. While no numerical estimate can be given, as yet, of the relation existing between heat and nervous force, there can be no doubt, however, that the latter, like all other kinds of energy, must be developed out of some equivalent amount of force, and leaves the body as such, or as some other mode of motion. That nervous force is developed out of heat appears very probable from the experiments of Lombard, already referred to, and by which it was shown that, while all mental action was accompanied with the production of heat, that more heat disappeared during deep thought than during reading to one's self, for example, of emotional poetry; further, it was shown by the same experimenter that more heat disappeared than when the reading was aloud—that is, had a muscular expression, part of the heat produced in the latter case being applied to making the oral or muscular effort. It is a matter of daily observation that silent grief is deepest, that pent-up emotion finds relief in physical action. This is in accordance with the results of the experiments just mentioned, since the heat that is transformed into emotions or ideas, in the one case, becomes muscular action in the other, and just in proportion as there is more of the one, so there is less of the other. Hirn<sup>1</sup> endeavored to determine, experimentally, the exact quantity of heat expended in the performance of mechanical work by comparing the heat produced within a definite time with the work done, the latter consisting in a man raising his own weight through a given height, the man walking upon the circumference of a tread-wheel rotating in the opposite direction to himself. According to Hirn, a man weighing 75 kilo., during an hour's work upon the tread-wheel, placed within the calorimeter, produced 430 heat units, whereas, judging from the amount of oxygen absorbed and carbonic acid exhaled, 500 heat units were produced. What, then, became of the 70 extra heat units? According to Hirn, it was at the expense of this amount of heat that the 29,610 kilogramme-metres of work were accomplished—that is, of raising 75 kilo. through nearly 400 metres ( $423 \times 70 = \frac{29610}{75} = 394$ ). On account, however, of the

errors incidental to the construction of the apparatus, and of the amount of heat produced as determined from the oxygen absorbed being estimated as too high, the results of Hirn, as just given, cannot be accepted; nevertheless, the difference between the amount of heat that appeared, as such, and that which ought to have appeared, can only be accounted for on the supposition that part of the heat produced was expended in the performance of mechanical work, and, as a corollary, it follows that less heat appears during a muscular contraction, when accompanied with work, than when without, and which accords with daily experience.

The relation that has been shown to exist between food, heat, and mechanical work, is not merely one of theoretical interest, but of practical importance. Suppose, for example, we wish to determine how much food—bread, for instance—is required to supply the force that will

<sup>1</sup> *Theorie mecanique de la Chaleur*, 3d ed., i. p. 35. Paris.



enable a man weighing 70 kilo. (154 pounds) to raise himself to about the top of Mont Blanc, a height of 4929 metres (15,774 feet), or to accomplish any other physical feat involving an equal expenditure of force. From the data given above such an estimate can be made, and in the following way: It being admitted that 1 heat unit, when applied mechanically, will raise 1 kilo. through 423 metres, it will require 11.6 times as much heat or 11.6 heat units to raise 1 kilo. 11.6 times as high, or 4906 metres ( $423 \times 11.6 = 4906$ ), and 812 heat units ( $70 \times 11.6 = 812$ ) to raise 70 times that weight, or 70 kilo. to the same height, 4906 metres (15,699 feet), or about that of Mont Blanc. That is, it is required to determine how much bread must be burned in the body to furnish 812 heat units, or the heat necessary when applied mechanically, to raise 70 kilo. (154 pounds) through 4906 metres (15,699 feet)—that is of doing an amount of mechanical work equal to 343,476 kilogramme-metres (1077 foot tons). By looking at Table LXVIII., it will be observed that while 1 gramme of dry bread crumb when burned out of the body produces 3.9 heat units, when burned in the body it produces 3.8 heat units; and when, further, it is remembered that of the heat produced by the burning of the food, only about one-ninth is expended in muscular work, the mechanical value of the 3.8 heat units is still further reduced to 0.4 heat unit ( $\frac{3.8}{9} = 0.4$ ): 1 gramme of

dry bread crumb when burned in the body furnishing then 0.4 heat unit for the production of muscular force, and 812 heat units being required, it is evident that 2030 grammes or 4 pounds of bread ( $\frac{812}{0.4} = 2030$  grs. = 4 lbs.) must be eaten to supply the necessary force

of raising 70 kilo. through 4906 metres; an estimate which agrees closely with that of Frankland,<sup>1</sup> according to that experimenter, 2.3 pounds of bread being required when oxidized in the body to raise 63.5 kilo. (140 pounds) through 3125 metres (10,000 feet) or 3.8 pounds of bread to raise 70 kilo. 4906 metres. It may appear at first sight strange that such an amount of muscular work can be performed upon a vegetable diet, but on reflection it will be remembered that the strongest men are not always meat eaters, and that among animals noted for their strength are the elephant and rhinoceros, strictly vegetable feeders. The heat developed during muscular contraction and its probable source will be considered more fully hereafter; the above examples will suffice, however, for the present, to illustrate the general relation existing between the loss of heat and the production of work.

It will be seen from Table LXX. that over ten per cent., or about one-ninth, of the heat produced is expended in muscular work, and it might appear at first sight that there would be no heat left available for the production of nervous force, as in mental effort. Apart, however, from the fact of the nervous and muscular force not being produced necessarily at the same time the estimates of the latter of 354

<sup>1</sup> Op. cit., Table iv. p. 197.

foot tons is too high, being equal to walking twenty miles a day. If, however, such an amount of exercise be taken, either little mental work can be done, or more food must be furnished than is ordinarily allowed a laboring man. It has already been mentioned that the temperature of the rectum is higher than that of the axilla, and from what has been said of the production and expenditure of heat it might be supposed that equal difference in temperature must prevail in other parts of the body, for although the circulating blood tends to equalize the temperature, nevertheless, on account of the radiation and conduction of the heat from the general surface varying so, the temperature can not be the same throughout the body. Such has been shown to be the case, experimentally. Thus, according to Davy,<sup>1</sup> while the temperature of the axilla, for example, was  $36.6^{\circ}\text{C}$ . ( $97.8^{\circ}\text{F}$ .), that of the lower part of the leg, and of the hollow of the foot amounted to only  $34.4^{\circ}\text{C}$ . ( $93.9^{\circ}\text{F}$ .), and  $32.2^{\circ}\text{C}$ . ( $89.9^{\circ}\text{F}$ .), respectively.

Having studied the manner in which animal heat is produced and expended, there remains now for our consideration the way in which animal heat is regulated, of determining as far as possible in detail the means by which the temperature of a hot-blood animal is maintained nearly constant, notwithstanding the variations in that of its surroundings. Among the conditions regulating animal heat may be mentioned the taking of solid and liquid food, the character of the respiration and circulation, the action of the skin, the influence of bodily size.

While the amount of heat produced will depend on the quality and quantity of the food, the mere taking of the latter in the form of hot or cold drinks, for example, with the view of increasing or diminishing the general temperature of the body, as is so commonly done, has already been mentioned as having really but little effect. In fact, as we have seen, about 2.7 per cent. of the heat produced is expended in warming all the solid and liquid food taken. The effect of cold drinks in lowering the general temperature of the body must therefore be but slight and temporary. On the other hand the effect of a hot drink, as we have seen, may be exactly opposite to what might have been expected, not only through the cooling effect due to the evaporation as in the drinking of hot tea, but on account of the specific substance of which the hot drink consists. Thus, for example, if hot spirits be taken, while at first a sense of warmth is experienced with the paralysis of the vaso-motor nerves by the alcohol, a greater quantity of blood flowing to the skin than usual, a proportionally larger quantity of heat will be lost from the general surface, and the effect of the hot drink will be in the long run, therefore, to lower the temperature of the body rather than to raise it. It has already been mentioned that about 4.1 per cent. of the heat produced is expended in warming the inspired air, and it might naturally be supposed that if the respiration be quickened and the amount of air inspired increased, that a proportionally greater quantity of heat would then be expended in warming it. Such would appear to be the case, dogs and other animals panting

<sup>1</sup> Phil. Trans., 1814, civ. p. 359.



when overheated. Not sweating except in those parts destitute of fur or hair, and the cooling effect of the perspiration being absent, the excess of heat developed is carried away in the expired air. The respiration when quick, will be more efficient, therefore, in lowering the general temperature of the body than when slow. Hence, also, the condition of heat dyspnœa or the rapidity of the breathing incidental to the exposure of the body to a high temperature. While no doubt under such circumstances a certain amount of heat is carried away in the expired air, and the temperature of the body prevented from rising as high as it otherwise would, it must be borne in mind that the quickened respiration in heat dyspnœa may be as much regarded as due to increased oxidation owing to the high external temperature as an effort of nature to prevent the temperature of the body rising too high. In other words, the cooling effect of the respiration is to be considered rather an incidental, not an invariable effect due to the activity of the oxidation caused by the external heat. In considering the cooling effect of respiration, it will be remembered, also, that 4.1 per cent. of the heat produced is expended in warming the inspired air. On account of so much heat being given off from the skin amounting through radiation, conduction, and evaporation, to nearly eighty per cent. of the heat produced, any change in the condition of the latter, as regards its structure or the amount of blood circulating through it, etc., will materially influence the general temperature of the body. Were the temperature of the skin constant, the amount of heat given off or taken up by it would depend simply upon that of the surrounding atmosphere, the skin losing heat if the temperature of the air was lowered, and gaining heat when that of the air was elevated. As a matter of fact, however, when the body is exposed to a temperature cooler than its own, the vessels of the skin contracting, the general surface becomes cooler, the difference between the temperature of the body and the surrounding air being diminished, the loss of heat is correspondingly diminished; on the other hand, when the body is exposed to a higher temperature than its own, the vessels of the skin expanding, the general surface becomes warmer, and a correspondingly greater amount of heat is lost.

It is a cause frequently of surprise to most persons to learn that, no matter how hot or cold they may feel, the temperature of their body nevertheless remains practically the same. From what has just been said, however, as regards the action of the skin in regulating the temperature of the body, it is obvious that in the cooling of the body through evaporation from the cutaneous surface, when exposed to a higher external temperature, the greater quantity of hot blood then circulating through the cutaneous vessels will, in impressing the sensory nerves, give rise to a general sense of warmth, so that while we feel warmer our body is actually getting cooler through the loss of heat involved in the evaporation. On the other hand, when, through the exposure to extreme cold, the cutaneous vessels are diminished in size, the smaller quantity of hot blood circulating through them will give rise to a sense of coolness, so that while we feel cool our body is actually becoming warmer through retention of the heat of the blood within it. The feeling warm or cold

depends, then, simply upon the relative amounts of blood circulating in the skin.

The effect of the successive exposure of the body to cold and heat, as just described, is well seen in the taking of cold baths. While in the bath, the vessels of the skin being contracted, the latter is pale and cold, the heat is retained, on emerging from the bath the vessels being dilated, the skin is red and warm, and heat is then given off from the surface. When we come to study the structure of the skin somewhat in detail, we shall see that its adipose tissue, being a bad conductor, prevents any great amount of heat from being given off from the inner parts of the body to the surface, and so lost.<sup>1</sup> This effect being especially well-marked in those cases where the difference in temperature on both sides of the skin does not amount to more than about  $9^{\circ}$  C. ( $16^{\circ}$  F.), the significance of the good effect of wearing clothing becomes apparent, since under such circumstances the body of a man is surrounded by a layer of air having a temperature of about  $30^{\circ}$  C. ( $86^{\circ}$  F.), the temperature under the skin being<sup>2</sup>  $36^{\circ}$  C. ( $96.8^{\circ}$  F.), this difference amounting, therefore, to only  $6^{\circ}$  C. ( $12.8^{\circ}$  F.) Clothing in man plays the same part as hair, fur, and feathers in animals, the air inclosed within the latter, through being a bad conductor, practically prevents any great loss of heat from the general surface. Man, however, is far better able to adapt himself to changes in climate than most animals, since through change of clothing, food, etc., and free action of the skin, he is able to live in tropical or temperate regions as well as in arctic ones.

It has already been mentioned that through the evaporation of the water from the skin as sweat about sixteen per cent. of the heat produced is expended, and that the amount of water evaporated will depend, among other conditions, upon the amount of water already existing in the atmosphere. It is very evident, therefore, that the regulation of the temperature of the body and the heat that a person can endure must soon reach a limit, since if the temperature of the surrounding air keeps continually rising, becomes saturated with watery vapor and is unchanged, the body, notwithstanding what has just been said of the action of the lungs, skin, etc., will become as hot as its surroundings. It is easier to keep out cold—that is, to keep in the bodily heat by proper food, clothing, and active exercise—than to keep out heat. Travellers, when well equipped, complain less of the cold of the arctic regions than of the heat of the tropics—indeed, the officers of the Austrian steamers say that while crossing the Red Sea, at certain seasons of the year, with all precautions taken, they at times fear they will lose their reason, the heat being so unendurable.

An important condition in the regulating of animal heat, and which may here be appropriately considered, is the influence of the size or bulk of the body of an animal as compared with its surface area; for the ratio of the bulk to the surface area being proportional to the size of the animal, and the heat produced being proportional about to the bulk, and the heat lost to the surface area, it follows that of two animals of similar

<sup>1</sup> Klug : Zeits. für Biologie, x. S. 73.

<sup>2</sup> Becquerel and Breschet : Ann. des Sciences Nat., 2ieme ser. t. iii. p. 257 ; t. iv. p. 243.



shape but of different sizes, that, other things being equal, the larger animal of the two will lose relatively the least heat. Suppose, for example, of two animals of similar shape, that one be ten times as long as the other, then, while the loss of heat in the larger animal will be as its surface area  $10^2$ , or 100 times as great as the small one, the heat produced by the larger animal will be at its bulk  $10^3$ , or 1000 times as great. It follows, therefore, that if two such animals have the same temperature that the small animal either retains its heat much better than the large one or that it produces heat far more actively. That the latter is the case appears from the fact of a small animal taking more food relatively than a large one, and of its circulation and respiration being absolutely more frequent. What has just been said of the laws of heat, as compared with its production, is further illustrated by a number of well-known facts. Thus small animals are more readily affected by changes in the external temperature than large ones, the temperature of a rabbit, for example, under such circumstances, varying more than that of a dog, that of a young animal more than that of an old one of the same kind, as that of the young child, as compared with that of the adult. Large animals, like the whale or hippopotamus, live either habitually or temporarily in the water, the latter being a better conductor of heat than air. On the other hand, the smallest homiothermal animals live in the tropics, while of animals of the same kind the largest ones live in temperate or cold regions. Of course, what has just been said with reference to the bulk and surface area in the production and loss of heat is not inconsistent with what daily observation teaches when man or animal changes the position of the body, for as the external temperature varies if the body, when cold, be contracted, less surface being then exposed less heat will be lost, whereas, if, when overheated, the body and limbs be stretched to the utmost, more surface being exposed, then more heat will be lost.

The influence exerted by the nervous system in the production and expenditure of animal heat, so far as known, will be considered hereafter. In concluding this part of our subject, however, it may be here said that, however accomplished, there undoubtedly exists some mechanism by which the production of heat in man and animals is adapted to that lost through the means already indicated. In addition to what has already been said, as a further confirmation of the existence of some regulating mechanism, may be mentioned the well-known facts already alluded to, of the diet of the inhabitants of cold countries being so different from that of those of hot ones, the amount of food consumed by the former not only being greater, but the food consisting largely of fat and oil, substances eminently suitable for the production of heat. A corresponding difference in diet is also made use of by the inhabitants of temperate regions in winter, as compared with summer, and with the same effect of increasing the production of heat in cold and of diminishing it in hot weather. It might be supposed that such a regulation of the heat produced and expended, of a loss of heat inducing an increased production, would be shown from the amount of oxygen absorbed and carbonic acid exhaled, and notwithstanding the numerous difficulties incidental to such an experimental investigation, it may be said that the

general result obtained by Lavoisier, Crawford, and De la Roche,<sup>1</sup> as well as by modern experimenters, as Rohring and Zuntz,<sup>2</sup> Colasanti,<sup>3</sup> Pflüger,<sup>4</sup> Prince Theodore,<sup>5</sup> Voit,<sup>6</sup> etc., was, as a rule, that the consumption of oxygen and exhalation of carbonic acid increased with a fall in the external temperature and diminished with a rise in it, though, under certain circumstances, hot-blooded animals behaved as cold-blooded ones—that is, the absorption of oxygen and exhalation of carbonic acid increase with a rise in the external temperature and diminish with a fall in it. Within certain limits at least, it may be said that, when a man or animal is exposed to cold, the production of heat is increased, as shown by the greater amount of oxygen absorbed and carbonic acid exhaled, but when exposed to heat the reverse is the case and less heat is produced.

<sup>1</sup> Op. cit.

<sup>3</sup> Ebenda, xiv. S. 92.

<sup>5</sup> Zeitschrift f. Biol., 1878, xiv. S. 51.

<sup>2</sup> Pflüger's Archiv, 1871, iv. S. 57.

<sup>4</sup> Ebenda, 1878, xviii. S. 247.

<sup>6</sup> Ebenda, S. 57.



## CHAPTER XXXIV.

### THE KIDNEYS AND URINE.

WE have seen that during digestion the food is transformed into albuminose, glucose, emulsified fats, etc., that through absorption and the circulation the latter are carried to the tissues, supplying the cells of the same with materials, which, either in being assimilated serve for repair, growth, or development, or in being destroyed are a source of heat and force; and that the destructive metamorphosis going on in the body caused by fermentation, hydration, oxidation, etc., incidental to life, the final outcome of which, at least, is the production of carbonic acid, water, and urea, is due, to a far greater extent, to the destruction of the food by the cells of the tissues than to the destruction of the tissues themselves; that, by means of the lungs, oxygen is introduced into the system, and carbonic acid and water removed, the skin, as we shall see, in the latter respect, acting also, to a certain extent, in the same way. In concluding now our account of nutrition, it remains for us still to consider the structure of the kidneys, and, so far as is known, the manner in which the urea, etc., are excreted by them from the system. It will be observed that we speak of the urea, etc., as being excreted by the kidneys, and it may be appropriately mentioned here that, while it would be equally correct to refer to the secreting, as well as to the excreting of the urine; the word secretion, however, is usually made use of in referring to a glandular product of some use, such as the saliva, gastric juice, etc., the term excretion being confined to products of no use, to be gotten rid of, such as the urine. In this sense, the bile, as we have seen, is both an excretion and a secretion.

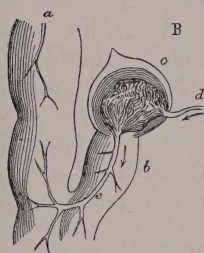
A kidney may be regarded, functionally, as consisting essentially of one or more tubes, opening externally at one end, but terminating internally at the other end in blind, sac-like capsules. The tubes and their capsules are lined with an epithelium, and covered more or less exteriorly with bloodvessels, the latter supplying the tubes with blood, from which are excreted, by the cells of their lining epithelium, the urea, water, etc., constituting the urine; elaborated and transported by the cells into the interior, or lumen of the tubes, the urine passes finally thence out of the body. Such a disposition as that just described, obtains in the kidneys of the lower vertebrates. In *bdellostoma*, for example, one of the cyclostomous fishes, the kidney consists (Fig. 258, *A*) of a ureter (*a*), from which are given off, at right angles, short uriniferous tubules (*b, b*), terminating in capsular-like Malpighian bodies (*c*), lined with an epithelium, and supplied externally with bloodvessels (Fig. 258, *d, e*). The kidneys in man, smooth, dark red, compressed, oval bodies, deeply set in the lumbar region, opposite the last dorsal and two or three upper lumbar vertebræ, measuring, on an average, 4 in. (10 cm.)

in length,  $2\frac{1}{2}$  in. (6 cm.) in breadth, and  $1\frac{1}{4}$  in. (3 cm.) in thickness, and weighing about  $4\frac{1}{2}$  ounces (121 grammes), present such a charac-

FIG. 258.

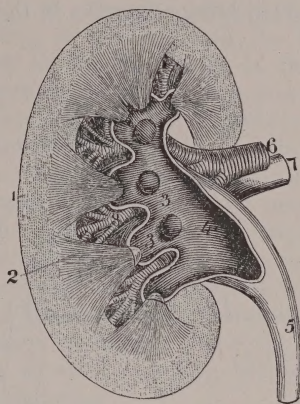


Kidney of bdellostoma.



The same magnified. (MÜLLER.)

FIG. 259.



Longitudinal section of a kidney 1. Cortical substance. 2. Renal pyramid. 3. Renal papillæ. 4. Pelvis. 5. Ureter. 6. Renal artery. 7. Renal vein. 8. Branches of the latter vessels in the sinus of the kidney. (LEIDY.)

teristic form through the presence of a deep notch on their inner side that the term reniform or kidney form, derived from them, is often conveniently made use of in describing various other natural objects. If a kidney be divided longitudinally through its breadth (Fig. 259), it will be observed that the hilus or notch leads into a cavity, the sinus of the kidney, which is filled in the natural condition with the pelvis (4), or expanded upper portion of the ureter (5), and the renal vessels (6, 7) and nerves. Such a section further shows that the kidney consists apparently, at least, of two distinct substances, an internal striated portion, the medullary substance (2), and an external granular-looking portion, the cortical substance (1). This distinction is, however, a purely artificial one, being, in reality, due to the uriniferous tubule (Fig. 260), coursing, in its beginning (9, 8), through the medullary or interior portion in a straight manner, but at its termination (5, 8), in the cortical or external portion in a convoluted one. Theoretically, at least, if the uriniferous tubules, of which the kidney largely consists, could be unravelled and straightened out, the distinction of medullary and cortical substance would then cease to exist. It is, also, very apparent, as observable in a longitudinal section (Fig. 259), that the interior, or so-called medullary portion of the kidney, is disposed in from ten to fifteen conical masses, the pyramids of Malpighi (2), so named after the celebrated anatomist of that name, the bases of which are imbedded in the cortical substance, while the free summits,



or papillæ (3), of the same project into the sinus of the kidney. It may be mentioned in this connection that the Malpighian pyramids, together with the cortical substance enveloping each of their bases, the columnæ, or septa Bertini,<sup>1</sup> correspond to the distinct lobules of which the human kidney consists in the foetal state, and while becoming indis-

FIG. 260.

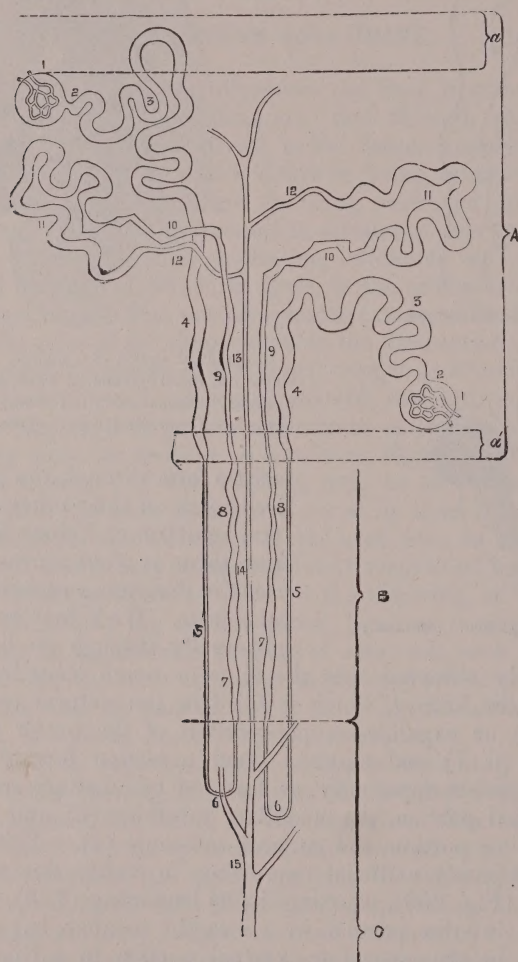


Diagram and course of two uriniferous tubules. A. Cortex. B. Boundary zone. c. Papillary zone of the medulla. a, a'. Superficial and deep layers of cortex, free from glomeruli.

solubly blended as development advances in man, remain quite distinct throughout life in many of the mammalia, as in the otter and bear among the carnivora, and in the cetacea—whales, dolphins, for example. If now the apex or summit of one of the Malpighian pyramids, or

<sup>1</sup> Mem. de l'Acad. des Sciences, 1744, p. 77.

papillæ, be examined microscopically, very minute orifices (between 200 and 500) will be observed, each of which is the beginning of a uriniferous tubule (Fig. 260), and which will be seen, if followed in longitudinal section, to pursue, as a tube of Bellini,<sup>1</sup> a nearly straight course through the medullary portion, as already mentioned, each Bellinian tubule, however, soon dividing and subdividing, the bundle formed by the division of the latter, at the beginning of the cortical substance, constituting the pyramids of Ferrein.<sup>2</sup> The uriniferous tubule followed thence outwardly toward the cortical substance, then turns back upon itself toward the medullary portion, and turning once more toward the cortical portion as the ascending and descending loops of Henle<sup>3</sup> becomes quite convoluted, constituting the cortical tubules of Ferrein,<sup>4</sup> terminating, finally, in a pouch-like dilatation, the capsule of Muller,<sup>5</sup> the latter, as we shall see, being inflected over the so-called Malpighian vascular glomerulus, the capsule and glomerulus together constituting a Malpighian corpuscle, as first described by Malpighi.<sup>6</sup>

The uriniferous tubules, held together by connective tissue, the stroma about  $\frac{2}{40}$  inches in length, and with a diameter varying between the  $\frac{1}{240}$ th and  $\frac{1}{600}$ th of an inch, the Bellinian tubules being the largest, consist of basement membrane lined with epithelium; the latter, however, like the diameter of the tube, differing considerably according to the part examined, being, for example, distinct and columnar, with a wide lumen in the straight, or Bellinian tubules, but indistinct granular, with little or no lumen in the convoluted tubules, or tubules of Ferrein.

The kidneys are very vascular, the arteries being large vessels in proportion to the size of the organs which they supply. The renal artery, Fig. 259, 6, as it approaches the hilus of the kidney subdivides into four or five branches, which, entering the sinus, pass thence between the pyramids into the substance of the kidney, dividing and subdividing as they ramify through the cortical substance, each branch finally terminating in an afferent vessel (Fig. 261, *a'*), leading to a Malpighian glomerulus, so called after their discoverer, Malpighi, around which, as already mentioned, as first shown by Bowman,<sup>7</sup> is inflected the capsule of Muller, the beginning or end, as you will, of the uriniferous tubule. Each Malpighian glomerulus (Fig. 261), about the  $\frac{1}{4}$ th of a mm. ( $\frac{1}{100}$ th of an

FIG. 261.

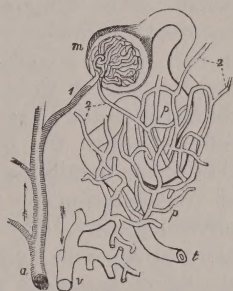


Diagram showing the relation of the Malpighian body to the uriniferous ducts and blood-vessels. *a*. One of the interlobular arteries. *a'*. Afferent artery passing into the glomerulus. *c*. Capsule of the Malpighian body. *t*. Uriniferous tube. *e'* *e'*. Efferent vessels which subdivide in the plexus *p*, surrounding the tube, and finally terminate in the branch of the renal vein, *e*. (BOWMAN.)

<sup>1</sup> Laurentii Bellini Exercitatio anatomica de structura et usu renum, pp. 64-72, Fig. x. Amstelodami, 1665.

<sup>2</sup> Mém. de l'Acad. des Sciences, 1749, p. 284, pl. 14 and 15.

<sup>3</sup> Abhand. d. K. Ges. d. Wiss. zu Göttingen, 1862, x.

<sup>5</sup> De glandularum secretorum structura penitior, p. 101. Lepsiae, 1830. / *delevis*

<sup>4</sup> Op. cit.

<sup>6</sup> Marcelli Malpighi Philosophii et Med. Bon E. Soc. Reg. Operum, tom. sec. Londini, 1686. De Renibus.

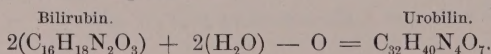
<sup>7</sup> Phil. Trans., 1842, p. 57.



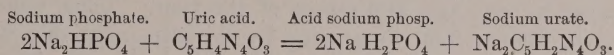
inch) in diameter, including the investing capsule, consists of a close-set, spheroidal, knot-like net of capillaries, from which emerge an efferent vessel  $e'$ , which, together with other efferent vessels, forms a capillary network ( $p$ ) along and between the uriniferous tubules. From this network the renal veins ( $e$ ) originate, which, converging, ~~form~~ <sup>from</sup> the external surface of the kidney toward the bases of the pyramids, pass through the sinus, and, becoming confluent, emerge as one trunk (Fig. 259, 7) from the hilus. The water, urea, etc., having been excreted by the epithelial cells lining the uriniferous tubules from the blood brought to them by the renal artery, elaborated as the urine, passes down through the uriniferous tubules, finally dribbling out of their orifices situated, as already mentioned, at the apices or summits of the Malpighian pyramids (Fig. 259, 3), one or more of the latter projecting into one of the calices or infundibula, into which the pelvis or upper expanded portion of the ureter (4) (within the sinus), is subdivided, a further passageway is provided by which the urine is conveyed to a temporary reservoir—the bladder—a musculo-membranous sac, from which it is finally eliminated during micturition from the body. The calices, pelvis of the ureter, and the ureter proper consist externally of a fibrous coat, of a middle unstriated muscular one, and internally of a lining mucous membrane. The fibrous layer of the calices at the base of the pyramid becomes continuous with that investing the sinus of the kidney, the latter, in turn, being a continuation of its external fibrous capsule; the middle muscular layer thinning away at the pelvis, disappears altogether at the base of the pyramids, while the mucous membrane of the calyx is reflected upon the pyramids, becoming continuous at the orifice with that of the uriniferous tubule. It is evident, therefore, ~~that~~ <sup>that</sup>, leaving out of consideration the anatomical details just described, ~~that~~ <sup>that</sup> a kidney, physiologically, may be regarded as consisting essentially of one or more uriniferous tubules, supplied with blood, a uriniferous tubule consisting of basement membrane separating blood on the one side from a secreting cell on the other. When reduced, therefore, to its simplest expression, the structure of the kidney does not differ in any way from that of glands in general.

#### THE URINE.

The urine is a clear, amber-colored fluid, of a watery consistence, containing a little mucus, saltish in taste, with a characteristic though not disagreeable odor, acid in reaction, and with a specific gravity varying between 1.020 and 1.025. The color of the urine appears to be due to a substance not yet satisfactorily isolated, but which, when slightly modified, gives rise to the substances variously known as urochrome, urosin, urosacin, hæmaphælin, urohæmatin, uroxanthin, urobilin, and hydrobilirubin, the latter terms indicating the affinity evidently existing between the coloring matter of the bile and that of the urine, whatever the latter may be, as seen by the readiness with which, by the addition of water and abstraction of oxygen, the coloring matter of the bile is transformed into that of the urine, or one of its modifications, as shown by the following formula:



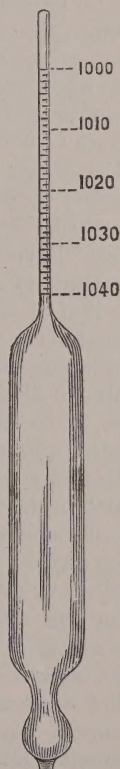
In all probability the coloring matter of the urine is derived from that of the bile, the varying tints often observed, from an amber color to red, being due to the oxidation of the former substance. The acidity of the urine is not due to free acid, as can be shown by there being no precipitate formed on the addition of sodium hypophosphite, but to the presence of the acid sodium phosphate,  $\text{NaH}_2\text{PO}_4$ , the latter salt being probably formed by the reduction of the basic sodium phosphate,  $\text{Na}_2\text{HPO}_4$ , of the blood by abstraction of one equivalent of its sodium by uric, hippuric, or carbonic acid, and sodium urate, hippurate, or carbonate, formed, as may be seen from the following formula, for example :



The acidity of the urine, due to acid sodium phosphate, as measured by the amount of a standard solution of caustic soda necessary to neutralize it, is equivalent to about three grammes of oxalic acid in twenty-four hours, supposing the urine voided in that time to amount to 1200 c. cm. The solution of soda, of such a strength that each cubic centimetre, containing 0.0031 gramme of soda, exactly neutralizes 0.0063 gramme of oxalic acid, is added, drop by drop, to a given quantity of urine—say 100 c. cm., until litmus paper changes violet in color, *i. e.*, neither to red nor blue. The number of cubic centimetres of the soda solution, as read off on the burette, say 30, when multiplied by 0.0063, will give then the amount of acidity, or 0.1890, in 100 c. cm. of urine, as measured in grammes of oxalic acid, and, consequently, of 2.2 grammes in 1200 c. cm.

The specific gravity of the urine, a matter of great importance practically, is readily determined by the urinometer (Fig. 262), the stem of which is so graduated that when immersed in water the level of the latter stands at that portion of the stem marked conveniently 1000, the level at which the urine stands, as read off on the urinometer when the latter is immersed in the urine giving the specific gravity sought. A convenient method of determining the solids of the urine, approximately, at least, is by means of what is generally known as Trapp's, or Christison's formula, based upon the fact, as empirically shown by that chemist, of the specific gravity of the urine bearing generally a close relation to the solid matters which it contains in solution. The rule is as follows: Multiply the last two figures (22) of a given specific gravity expressed in four figures—say 1.022, by 2.33; the result,  $22 \times 2.33 = 51.26$  grammes, will be the amount of solids contained in 1000 parts of urine having a specific gravity of 1.022, and if the urine passed in twenty four hours amounts to 1200 c. cm., then the solids will be increased proportionally,  $1000 : 1200 :: 51.26 : x = 61.51$

FIG. 262.

Urinometer.  
(LANDOIS.)



grammes. If the specific gravity of the urine be below 1.018, greater accuracy will be obtained by multiplying by 2 instead of 2.33.

The daily quantity of urine excreted amounts in the adult man, on the average, according to Parkes,<sup>1</sup> who has compared the observations of many observers, to about fifty-two and a half fluid ounces. As little as thirty-five ounces, and as much as eighty-one ounces may, however, be voided within the limits of health, and it may be added that almost every intervening number between these limits has been given as the usual average, the very greatest difference prevailing in this respect. Apart, however, from personal peculiarities, the amount of urine excreted is also influenced by sex, age, and season of the year. Thus, more urine is excreted by women than men, more by children, relatively to their weight, than by adults; more in winter, the skin being then less active, than in summer. When it is considered that the quantity and quality of the urine, as we shall see, are influenced by such conditions as wakefulness, sleep, rest, exercise, solid and liquid food, it might be naturally supposed that considerable differences would present themselves in the urine passed at different times during the day, usually five or six times within the twenty-four hours. As a matter of fact, diurnal variations do succeed each other quite regularly. Thus, the urine collected during the night and voided early in the morning, is strongly colored, distinctly acid, and of a high specific gravity; toward noon it becomes paler, less dense (1.003 to 1.008), and less acid, the acidity even disappearing altogether; during the afternoon and evening, the color, density, and acidity increase, while by night it has become again highly colored, markedly acid, and with a specific gravity of 1.028 or even 1.030. As these diurnal variations are, however, increased or diminished by the amounts of liquids taken, and as the acidity of the urine is inversely as that of the stomach, and may be more or less neutralized by fruits, vegetables, etc., the lactates, malates, and tartrates of the same being replaced within the system by carbonates, and reappearing in that form in the urine, it is evident that if the acidity and specific gravity are to be determined, one sample voided will not suffice, but that the entire quantity passed in twenty-four hours should be examined, and the mean result taken. It is worth while mentioning that with reference to the liquids absorbed by the system or lost, that under normal conditions the relation of the specific gravity of the urine to that of the liquids is an inverse one. Thus, if a great quantity of liquid be taken, or the perspiration be diminished, the amounts of solids remaining the same, the specific gravity of the urine will be diminished, whereas, if drinks be abstained from, or the perspiration be increased, the specific gravity will be increased. If, however, notwithstanding that a great quantity of liquid be absorbed, the specific gravity still remains high, or with a diminution in the liquid the specific gravity remains low, there would be reason to suspect disease through the increase or diminution respectively in the solid constituents of the urine, and such would also be the case if, the specific gravity remaining constant, the quantity of urine increased or diminished, and *vice versa*.

<sup>1</sup> On the Urine p. 5. London, 1860.

TABLE LXXI.<sup>1</sup>—CONSTITUENTS OF URINE AND AMOUNTS EXCRETED IN TWENTY-FOUR HOURS.

| Constituents.                | Average quantity excreted in 24 hours in grains. | Average quantity excreted in 24 hrs. in grs. for each 1 lb. of body weight (150). |
|------------------------------|--------------------------------------------------|-----------------------------------------------------------------------------------|
| Urea . . . . .               | 512                                              | 3.5                                                                               |
| Uric acid . . . . .          | 8.5                                              | 0.057                                                                             |
| Allantoin . . . . .          | Trace.                                           | ...                                                                               |
| Hippuric acid . . . . .      | 15                                               | 0.1                                                                               |
| Kreatinin . . . . .          | 15                                               | 0.1                                                                               |
| Sugar . . . . .              | ...                                              | ...                                                                               |
| Xanthin . . . . .            | ...                                              | ...                                                                               |
| Paraphanic                   | acids. . . . .                                   | Traces.                                                                           |
| Kryptophanic                 |                                                  |                                                                                   |
| Phenylic                     |                                                  |                                                                                   |
| Taurylic                     |                                                  |                                                                                   |
| Damaluric                    |                                                  |                                                                                   |
| Damolic                      |                                                  |                                                                                   |
| Fatty                        |                                                  |                                                                                   |
| Oxaluric                     |                                                  |                                                                                   |
| Oxalic                       |                                                  |                                                                                   |
| Pigment . . . . .            | 7                                                | .....                                                                             |
| Mucus . . . . .              | ...                                              | .....                                                                             |
| Inorganic salts, composed of | 140.00 to 380.00                                 | 0.933 to 2.53                                                                     |
| Sulphuric                    | 17.34 to 41.14                                   | 0.115 to 0.27                                                                     |
| Phosphoric                   | 31.00 to 79.00                                   | 0.207 to 0.526                                                                    |
| Nitric                       | Traces.                                          | .....                                                                             |
| Silicic                      | Traces.                                          | .....                                                                             |
| Chlorine . . . . .           | 51.87 to 173.2                                   | 0.345 to 1.154                                                                    |
| Potassium . . . . .          | 26.36 to 107.7                                   | 0.175 to 0.718                                                                    |
| Sodium . . . . .             | 79.75 to 171.0                                   | 0.531 to 1.14                                                                     |
| Calcium . . . . .            | 2.33 to 6.36                                     | 0.015 to 0.042                                                                    |
| Ammonium . . . . .           | Trace.                                           | .....                                                                             |
| Magnesium . . . . .          | 2.53 to 4.21                                     | 0.016 to 0.028                                                                    |
| Iron . . . . .               | Trace.                                           | .....                                                                             |

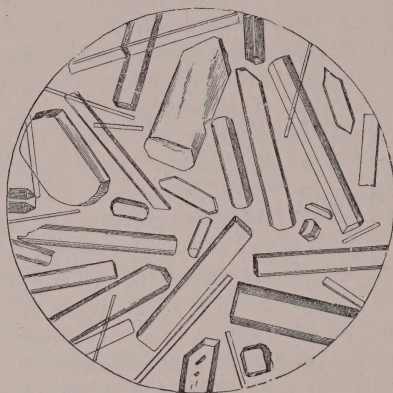
The urine conveying out of the body, as we have seen, many of the proximate principles to their derivatives, the latter having played their part in the economy, must necessarily be a highly complex fluid consisting of both organic and inorganic principles. That such is the case is evident from the composition of the urine as given in Table LXXI., after Carpenter, based principally upon the works of Parkes,<sup>2</sup> Thudichum,<sup>3</sup> Neubauer,<sup>4</sup> and Vogel. Of the various constituents of the urine, whether organic or inorganic, urea existing in about 2.6 parts per hundred, about half the solid matters of the urine, is the most important. Urea consists of carbon, oxygen, nitrogen and hydrogen united in the proportions shown in the formula  $\text{CON}_2\text{H}_4$ , and is isomeric, therefore, with ammonium cyanate,  $\text{NH}_4\text{CNO}$ . Urea is, however, regarded by chemists as being carbamide or the diamide of carbonic acid as expressed in the formula  $\text{CO} \begin{Bmatrix} \text{NH}_2 \\ \text{NH}_2 \end{Bmatrix}$  Urea is a colorless neutral substance, very soluble in water and boiling alcohol, but insoluble in ether, and crystallizing in four-sided prisms (Fig. 263). Urea can be

<sup>1</sup> Carpenter's Physiology, 1881, p. 468.<sup>2</sup> On the Pathology of the Urine. London, 1858.<sup>3</sup> On the Urine, New Syd. Soc. Trans. London, 1863.<sup>4</sup> Op. cit.



readily obtained from the urine in the following manner. Add, say, half a drachm of pure nitric acid to a drachm of concentrated urine in a watch glass and set aside to cool. The nitrate of urea then formed will be precipitated as a yellow crystalline mass. The insoluble nitrate

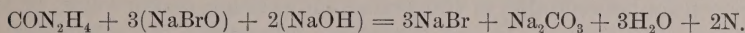
FIG. 263.



Urea, prepared from urine, and crystallized by slow evaporation. (LEHMANN.)

caught on a filter, dried, and dissolved in boiling water, is mixed with animal charcoal to remove coloring matters and filtered while hot. The filtrate being then allowed to cool, colorless crystals of nitrate of urea will be deposited. The latter being dissolved in boiling water and barium carbonate added as long as effervescence takes place, barium nitrate and urea will be produced, from which after evaporating to dryness the urea can be extracted with absolute alcohol. On evaporating the alcoholic solution of urea crystals of pure urea are obtained. As may be seen from Table LXXI., as much as 512 grains of urea are excreted on an average daily, which, consisting of 46.6 per cent., or 235 grains, nitrogen, may be regarded as the chief especial product of the oxidation of the nitrogenous food or tissue, or both, and to a great extent taken as the measure of the disintegration of the same, since with the above amount of urea, the amount of nitrogen excreted by the skin and in the feces would amount to only about 0.6 grain and 18 grains respectively. It is, therefore, of great importance that we should have some ready method of determining the amount of urea present in a given quantity of urine. Of the different methods in use none is more convenient or more accurate than that of Davy, based upon the decomposition of urea by sodium hypobromite—the nitrogen of the urea being set free, and with caustic soda in excess, the carbonic acid developed combines with the soda, the water being retained in the mixture; the amount of urea is determined by the amount of nitrogen evolved. The experimental procedure is as follows: A given quantity of urine, say 4 c. cm., is placed within the vessel, and about 25 c. cm. of a solution of sodium hypobromite freshly made by dissolving 100 grammes of caustic soda in 250 c. cm. of water, to which are added 25 c. cm. of bromine in

the vessel. The immediate effect of the mixing of the urine with the hypobromite is the development of N, as seen from the following reaction:



The free nitrogen passing into and being collected by the graduated tube standing over mercury, will be found to amount to 30 c. cm., supposing at the moment of the experiment the thermometer registers 15° C. (59° F.), and the barometer 740 mm. (29.6 in.), or 27.6 c. cm. if the volume of 30 c. cm. be corrected for temperature and pressure by the methods already explained. Now, since 100 grammes of urea contain 46.6 gr. of nitrogen, 1 gramme of urea will contain 0.466 of a gramme of nitrogen, and as 1000 c. cm. of nitrogen weigh 1.252 grammes, 372 c. cm. of nitrogen will weigh proportionally 0.466 of a gramme; but as 0.466 of a gramme of nitrogen corresponds to 1 gr. of urea, the latter will give off 372 c. cm. of nitrogen, and the 0.0027 of a gramme of urea proportionally 1 c. cm. of nitrogen. If now the 27.6 c. cm. of nitrogen collected in the graduated tube given off from the urine be multiplied by 1.0027, or the amount of urea in grammes corresponding to a cubic centimetre of nitrogen at standard temperature and pressure, the product, 0.0745 gramme, will be the amount of urea in 4 c. cm. of urine, and consequently 34 grammes (524 grains) in 1300 c. cm. of urine, or the amount, say, passed in twenty-four hours. Such a rough and ready method for the determination of urea as that just given, like all other similar ones, is open to some criticism, the most important of which is, that uric acid and other nitrogenous principles present in the urine, like urea, are also decomposed by hypobromites or hypochlorites, the latter being used as well as the former to free the nitrogen. The quantity of such nitrogenous principles is, however, so small that the error introduced can be neglected without materially affecting the accuracy of the result.

While the urea excreted by an adult amounts on an average in 24 hours, as has already been mentioned, to about 512 grains, it must be mentioned that the quantity eliminated varies very considerably with the age, weight of body, sex, period of the day, season, and kind of food. Thus children of from three to seven years of age, weighing say, 30 lbs., in daily excreting, may be, 240 grs. of urea, eliminate more than half that excreted by an adult, 459 grains, weighing, however, 153 pounds, or more than five times as heavy. In other words, while an adult man excretes for each pound of body weight about 3 grs. of urea, a boy excretes 7.5 grs., or more than twice as much. As might be expected, therefore, the amount of urea excreted continues to diminish as age advances. It would appear that less urea is excreted by the female than the male in the proportion, perhaps, of about half a grain less in the female for each pound of body weight, and that the amount is diminished during menstruation. The hour of the day apparently also exerts an influence upon the excretion of urea, the greatest amount being eliminated after breakfast and tea, the least during the night. The increase or decrease observed may be, however, due, to a certain extent, as we shall see, to the taking of or the abstaining from food. Like the urine, more urea is probably eliminated in cold than in warm weather.



It is difficult, if not impossible, to give exact numerical estimates. According to Dr. E. Smith,<sup>1</sup> the daily variations in himself amounted in a year from between 219 to 700 grains, the average, on the whole, being, however, 519 grains. Of the conditions influencing the production of urea, none is so important as that of the taking of food. This becomes at once evident when the amount of urea excreted upon a vegetable or mixed diet is compared with that of a highly animal one. Thus while the urea excreted by Ranke,<sup>2</sup> during 24 hours on a vegetable diet, amounted to only 264 grains, and on a mixed to between 463 and 617 grains, on a highly animal diet it was increased to as much as 1332 grains, or nearly three times as much as normal. From such facts as that nearly all of the nitrogen of the food consumed passes out of the body in the form of urea in the urine, each grain of urea implying the disintegration of 3 grains of albuminous matter, or about 15 grains of meat, and that the amount of urea excreted attains its maximum within five to seven hours after the taking of food, it would appear that by far the greatest amount of the urea produced must be derived directly from the disintegration of the albuminous, nitrogenous food brought about through fermentation, oxidation, etc., as already mentioned, it being absurd to suppose that of the five pounds of meat eaten by a large dog, to take an extreme instance, the albuminous matter of the same should be first transformed into tissue, then decomposed into urea, and eliminated by the kidneys within the short space of 24 hours. It appears to us at least more reasonable to suppose that the albumen of the food goes through the system like a dose of salts, so to speak, with the difference, however, that the albumen entering the body as such in the food, leaves it in the excreta as urea, carbonic acid, and water. If the above view of urea being derived from nitrogenous food rather than nitrogenous tissue be accepted, it is readily understood why muscular exertion does not increase, as was once supposed, the production of urea, for muscular force, being like all other kinds of so-called vital force, transformed heat, and the latter being developed, if not exclusively, at least to a greater extent out of fats and carbohydrate than albuminous food, it follows that muscular activity will be measured not by the amount of urea but by that of the carbonic acid produced. Such theoretical considerations are fully borne out by the experiments of Smith, Lehmann, and Voit. In the celebrated ascension of the Faulhorn by Fick and Wislicenus,<sup>3</sup> in 1866, involving considerable muscular exertion, as may be imagined, it will be seen from Table LXXII. that so far from the urine being increased during the period of ascent, lasting 8 hours and 10 minutes, and the 6 hours immediately following, as measured by the nitrogen eliminated, it was actually diminished, since while during the 12 hours preceding the ascent the urea excreted by Fick, for example, measured by the 106.7 grs. of nitrogen eliminated, would amount to about 228 grs. during the period of 14 hours, including not only the 8 hours of work in the ascent but the succeeding 6 hours of rest, it would amount to only 190 grs., as measured by the 88.6 grs. of nitrogen eliminated.

<sup>1</sup> Proc. of Royal Soc., May 30, 1861. Carpenter's Physiology, 1881, p. 470.

<sup>2</sup> Physiologie, 1872, S. 509.

<sup>3</sup> London Phil. Magazine, 1866, p. 485.

TABLE LXXII.<sup>1</sup>—ASCENT OF THE FAULHORN (6417.5 FEET).

Weight of Fick, 145.5 lbs.  $\times$  6417.5 = 933746 foot pounds.  
 " " Wislicenus, 167.5 lbs.  $\times$  6417.5 = 1074931 " "

|                                          | Grains of nitrogen excreted by     |      |             |      |
|------------------------------------------|------------------------------------|------|-------------|------|
|                                          | Fick.                              |      | Wislicenus. |      |
| Night urine previous to ascent . . . . . | 106.7                              |      | 103.2       |      |
| Work 8 hours 10 min. . . . .             | 51.1                               |      | 48.3        |      |
| After work 6 " . . . . .                 | 37.5                               | 88.6 | 37.3        | 85.6 |
| Night (after a meal) 10½ hours . . . . . | 74.3                               |      | 82.5        |      |
| 88.6 grs. N of Fick . . . . .            | derived from 575.0 grs. of muscle. |      |             |      |
| 85.6 " " Wislicenus " . . . . .          | 555.5                              | "    | "           | "    |
| 575.0 grs. of muscle of Fick . . . . .   | burned raised 498525 lbs. 1 foot.  |      |             |      |
| 555.5 " " " Wislicenus " . . . . .       | "                                  | "    | 481618      | "    |
|                                          | Fick.                              |      | Wislicenus. |      |
| Work of ascending mountain . . . . .     | 933746                             |      | 1074931     |      |
| " " circulation . . . . .                | 183348                             |      | 213906      |      |
| " " respiration . . . . .                | 37620                              |      | 43890       |      |
| " " foot pounds . . . . .                | 1154714                            |      | 1332727     |      |
| " done from burned muscle . . . . .      | 498525                             |      | 481618      |      |
| " " unaccounted for . . . . .            | 656189                             |      | 851109      |      |

It being borne in mind that no albuminous food had been taken for seventeen hours previous to the ascent by Fick or Wislicenus, their diet consisting of cakes made out of fat, starch, and sugar, it is not strange that the amount of urea excreted should have been small, it being derived from the albuminous tissues of the body; the latter supplying the albuminous food that would have been otherwise present had the diet been a mixed one. It is well known that, even in starvation, more urea is excreted than on a diet consisting of sugar, fat, etc., since the latter substances, in supplying ready materials for combustion, spare the tissues of the body.

That there is an enormous amount of potential force locked up latent, so to speak, in sugars, etc., is made evident in the extreme weakness and emaciation so noticeable in diabetes, since the sugar in that disease, instead of being burned, and constituting as normally a source of heat and force, passes unoxidized out of the body. The amount of force lost to the system under such circumstances may be judged of when it is remembered that in extreme cases of diabetes as much as 40 ounces of sugar are passed in the urine in twenty-four hours, and that if the 16 ounces of carbon contained in such an amount of sugar were oxidized, heat enough would be produced, if applied mechanically, to raise 20 millions of pounds 1 foot high,<sup>2</sup> or carry a man weighing 130 pounds on a level 66 miles. The system being deprived, therefore, in this disease of such a source of force, draws upon the albuminous tissues, hence the characteristic emaciation and weakness. It is evident, also, as may be seen from Table LXXII., on the supposition that the combustion of muscle is the source of its power, that the burning of 575

<sup>1</sup> Letheby On Food, p. 64. London, 1872.

<sup>2</sup> H. Bence Jones: Pathology and Therapeutics, p. 73. London, 1867.



grains of the muscular tissue of Fick's body, as implied in his elimination of 88.6 grains of nitrogen, would not suffice, in his case, to account for the work actually performed by him in ascending the Faulhorn by 656,189 foot-tons, and the same is true by almost as large an amount in the case of Wislicenus, the work unaccounted for being evidently due to the heat developed through the combustion of the starch, sugar, and fat. Essentially the same result was obtained more recently by Houghton,<sup>1</sup> who found, while walking five miles a day, that the urea eliminated amounted to 501.28 grains; that when the walk was increased to 20.74 miles a day, and kept up for five consecutive days, the urea eliminated amounted to only 501.16 grains, or actually less. Parkes<sup>2</sup> found, also, that in the case of two soldiers, who walked in two days 56 miles on a non-nitrogenous diet, that the total increase of nitrogen eliminated amounted, in the one case, to only about 3 grains; and, in the other, 15 grains; corresponding to an increase of 6.4 grains, and 32.1 grains of urea, respectively, in forty-eight hours. The case of Weston, who walked over 300 miles in five consecutive days, cited by Flint<sup>3</sup> as an illustration of urea being increased by muscular exercise, illustrates really only what we have already seen to be the case, that the amount of urea excreted is greatly increased upon a highly nitrogenous diet, and that heat, the ultimate source of muscular force, can be developed through the combustion of albuminous, as well as of fatty or carbohydrate foods, the former means of obtaining the necessary heat being, however, a far more expensive way than the latter, and entailing greater work upon the system. It is true that, if the coal gives out, the steamer can be supplied with fuel from its masts, shrouds, etc., and other integral parts of its structure; one does not resort, however, save in dire necessity, to such a source of fuel. The facts of the case of Weston, just referred to, are essentially as follows: Weston walked in five consecutive days 310 miles, losing in weight  $3\frac{1}{4}$  pounds. 1173.80 grains of nitrogen were taken into the system in the food, and 1807.60 grains were eliminated from it in the excreta, leaving 633.80 grains of nitrogen to be accounted for, which were evidently derived from the 3 pounds of tissue lost, the latter containing 633.80 grains of nitrogen; the remaining quarter of a pound, lost in weight, corresponded, probably, to the production of water or fat. Such being the case, and Weston being trained down, and having, therefore, little, if any, superfluous fat or carbohydrate matter at disposal for the production of heat or force, it would appear, from the large quantity of nitrogen eliminated, that his albuminous tissues were largely drawn upon to supply, through combustion, the heat incidental to the production of such a muscular effort. The 3 pounds of muscular tissue lost by Weston during the walk, supplied, therefore, the body with 3 pounds of albuminous food, which, in being consumed, accounted for the elimination of 633.80 grains of nitrogen, corresponding to 1124 grains of urea, just as if he had eaten 3 pounds of butcher's meat, instead of the same amount of his own body. That this conclusion is not merely a theoretical one is shown by the

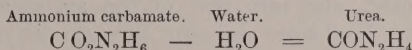
<sup>1</sup> British Medical Association, 1868.

<sup>3</sup> New York Medical Journal, 1871, p. 687.

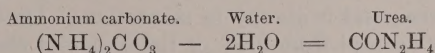
<sup>2</sup> Proc. Royal Soc., 1867, No. 89, 94.

fact of Rubner,<sup>1</sup> weighing 158 pounds, being able to consume 2.87 pounds of meat, of which 2.84 were perfectly destroyed in the system, giving rise to a corresponding quantity of urea and nitrogen.

Not only has it been held that muscular activity increases the amount of urea, but mental and sexual activity as well. Even if such is shown, hereafter, to be the case, apart from the influence exerted by nitrogenous food, the facts are, at present, too few to offer any exact numerical estimate. It would appear, from what has just been said with reference to the production of urea, that, to a large extent at least, it is derived directly from the nitrogenous principles of the food without the latter becoming first tissue; and while, in all probability, such is the case, it must be admitted that exactly how or where the transformation of food into urea takes place has not, as yet, been positively established. It will be remembered, however, that, in speaking of intestinal digestion, leucin and tyrosin were mentioned as being among the products of the action of the pancreatic juice upon the albuminous principles of the food, and that, together with the latter, the glycin of the decomposed glycocholic acid of the bile was reabsorbed. Now leucin,  $C_6H_{11}(H_2N)O_2$ , being amido-caproic acid—that is, caproic acid,  $C_6H_{12}O_2$ , in which an atom of hydrogen is replaced by the residue of ammonia,  $H_2N$ , and tyrosin,  $C_7H_5(C_2H_5HN)O_3$ , being amido-ethyl salicylic acid—that is, salicylic acid,  $C_7H_6O_3$ , in which an atom of hydrogen is replaced by the residue of ethylamin, or  $C_2H_5HN$ ; glycin,  $C_2H_3(H_2N)O_2$ , being amido-acetic acid—that is, acetic acid,  $C_2H_4O_2$ , in which an atom of hydrogen is replaced by the residue of ammonia; it is readily conceivable how, through the disintegration of these substances, leucin, tyrosin, and glycin, urea could be formed by simply supposing that the residue of ammonia,  $NH_2$ , or of ethylamin,  $C_2H_5HN$ , entering into their composition, is set free, becomes  $NH_3$ , or ammonia, and then combines with carbamic acid,  $CO_2NH_3$ , with subsequent dehydration, as follows:



the caproic, salicylic, and acetic portions of the leucin, tyrosin, and glycin respectively being oxidized into water, or, in the case of the caproic acid, into fat. Or what is also probable, that ammonium,  $NH_4$ , being developed in the disintegration of the albuminous food in combining with a carbonic acid radical,  $CO_3$ , with subsequent dehydration, would give rise to urea as follows:



or with that of cyanic acid,  $CNO$ , to form ammonium cyanate,  $NH_4CNO$ , which is isomeric with urea. As a confirmation of the view that leucin and glycin are antecedents of urea, it may be mentioned that feeding dogs<sup>2</sup> with the same increases the amount of urea.

There being no difficulty in comprehending how urea may be

<sup>1</sup> Zeitschr. für Biologie, 1879, xv. S. 122.

<sup>2</sup> Schultzen and Nencki: Zeit. für Biologie, 1872.



developed out of the albuminous principles of the food or their ammoniated derivatives—it remains, therefore, only to show where the transformation takes place. Now, from such facts as that of the liver containing more urea than any other gland in the body, as shown by Meisner,<sup>1</sup> of the albuminous principles of the food, of the glycine of the decomposed bile, of the leucine and tyrosine of the spleen being carried by the portal circulation to the liver, of leucine and tyrosine replacing urea in the urine in acute atrophy of the liver, the conclusion forces itself upon us that it is the liver that elaborates the urea out of the albuminous principles of the food, etc., brought to it by the portal circulation. Admitting that by far the greatest quantity of urea is derived from the transformation of albuminous food in the liver, it must be remembered that urea is not only found in the liver, but in many other parts of the system—in the chyle, saliva, blood, serous fluids, etc., and that in starvation in the absence of all food, though the amount of urea is gradually diminished, it is nevertheless present, even to the last. Of course, in such cases, as already mentioned, one part of the body being nourished at the expense of another, the nitrogenous tissues, instead of food, supply the materials for the development of urea. Urea being found under normal circumstances in many parts of the system, and being derived in starvation from the tissues, it is reasonable to suppose that part of the urea is also derived from the latter even when nitrogenous food is taken, and since leucine and tyrosine are found in the thyroid, thymus, parotid, and submaxillary glands, kidney, liver, and suprarenal capsules, as well as in the pancreas and spleen, analogy would lead us to suppose that they may be antecedents of the urea derived from tissue, as we have supposed them to be of the urea derived from food. In this connection it is an interesting fact that while urea is not found in the muscles, spleen, or nervous tissue, kreatine,  $C_4H_9N_3O_2$ , enters into the composition of muscles to the extent of two per cent., and into that of the spleen and probably of nervous tissue also. Now since kreatine, through dehydration, readily becomes kreatinin,  $C_4H_7N_3O$ , and the latter through oxidation, urea,  $CON_2H_4$ , it is quite probable that kreatine may be an antecedent of urea arising out of the disintegration of the muscular tissues, etc., but converted into urea elsewhere. It should be mentioned, however, that the kreatine, or rather kreatinin, normally found in the urine is not that of the muscular tissue, etc., just alluded to, but is probably derived from the food, since it varies in quantity, increasing with a meat diet, but not with exercise, and is absent in starvation. On the supposition that urea, whether derived from food or tissue, is not elaborated by the kidneys, but simply excreted out of the blood brought to them, we might expect to find that the blood of the renal artery contained more urea (0.03 per cent.) than that of the renal vein (0.01 per cent.), but also with the extirpation of the kidneys, or the ligation of the ureters, which has practically the same effect, that the urea would accumulate in the blood, and such has been found to be the case according to Grehan<sup>2</sup> and Gscheidlen<sup>3</sup>, the amount being increased from 0.026 to

<sup>1</sup> Centralblatt med. Wiss., 1870, S. 249.

<sup>2</sup> Zeits. für nat. med., xxxi. S. 144.

<sup>3</sup> Studien u. d. Ursprung d. Harnstoffs, Leipsic, 1871; also Centralblatt, 1871, p. 630.

206 per cent. in twenty-four hours, while Voit<sup>1</sup> obtained after extirpation of the kidneys in an animal 5.3 grammes of urea, or almost the same amount as would have been normally excreted (5.8 grammes) in the same time. It may be mentioned that the toxic effects appearing under such circumstance appear to be due, not so much to the accumulation of a great quantity of urea as to the retention within the system of other undefined albuminous substances.

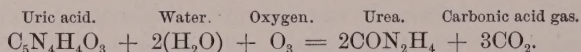
<sup>1</sup> Centralblatt, 1868, p. 468.



## CHAPTER XXXV.

### THE URINE.

OF the remaining constituents of urine, next in importance to urea, as representing, like it, the result of the metamorphosis of nitrogenous food and tissue, is uric acid,  $C_5H_4N_4O_3$ . Chemically, uric acid may be regarded as imperfectly oxidized urea, a molecule of uric acid, through oxidation in presence of water, being transformed into two molecules of urea and three molecules of carbonic acid, the carbonic oxide constituent of the uric acid being oxidized as follows:



It does not, however, follow that uric acid is invariably an antecedent of urea. Indeed, the production of uric acid and urea does not depend, according to many physiologists, so much upon the presence of oxygen as upon the structure of the uriniferous tubules, and the amount of water absorbed, the physical conditions involved in some animals being better adapted to the excretion of uric acid, and in others to that of urea. That the amount of uric acid and urea respectively produced does, however, depend to a great extent upon the amount of oxygen absorbed, appears from the striking contrast offered by reptiles and mammals when considered in this respect. Thus, while in reptiles, in which respiration is inactive, uric acid is the principal nitrogenous constituent of the urine, urea being absent; in mammals, on the contrary, in which respiration is active, urea is the most important of the nitrogenous constituents, uric acid being found in small quantities, both absolutely and relatively with reference to the urea; in man, for example, about 8.5 grains of uric acid only being excreted in twenty-four hours, or one part of uric acid to about sixty parts of urea, as may be seen from Table LXXI. The view of the production of uric acid instead of urea being due to defective oxidation, has been held, however, by many physiologists to be inconsistent with the fact that, while the respiration in birds is more active even than that of mammals, the urine of these animals, nevertheless, contains uric acid and urates instead of urea, as in reptiles. A little consideration will show, however, that, notwithstanding the activity of their respiration, their economy is such that it is an advantage to birds, this retention of the ancestral trait (birds being only highly specialized reptiles) of producing uric acid and urates instead of urea. Thus, as urged by Odling,<sup>1</sup> while the respiration of birds is very active, it is not excessive, when considered with reference to the great

<sup>1</sup> Animal Chemistry, p. 142. London, 1866.

need of oxygen experienced by these animals, birds being more dependent on a constant supply of pure air than any other animals. Their organization is, therefore, such that, while, on the one hand, the respiratory surface is increased in every possible way, notably so in the predatory birds, on the other hand, through the excretion of uric acid, instead of urea, the demand for fresh air is diminished, less oxygen being required for the conversion of the carbon of the food or tissue into the carbonic oxide (CO) constituent of hydrated uric acid,  $C_3O_3 \cdot 2(CN_2OH_4)$ , than into carbonic acid,  $3(CO_2)$ , and urea,  $2(CON_2H_4)$ , which hydrated uric acid becomes through oxidation, and, consequently, less heat or force is lost in elevating the temperature of the inspired air to that of the body, an additional advantage. It might appear at first sight, though, that the heat developed through the oxidation of carbon into carbonic oxide (CO) would be only one-half that developed in the production of carbonic acid ( $CO_2$ ). It must be remembered, however, that the heat absorbed in the conversion of carbon into carbonic acid gas is lost to the economy, and that, therefore, the difference in the heat developed (about 25 per cent.) in the two cases is not as great as might have been supposed, and that the amount of oxygen is also employed with far less economy in the production of  $CO_2$ , than in that of CO, the ratio being as 1 to  $1\frac{1}{2}$ .<sup>1</sup> Further, the proportion of nitrogen to carbon in ammonium urate,  $C_5N_5H_7O_3$ , being as 1 to 1, whereas, in urea,  $CON_2H_4$ , it is as 1 to 2, it follows that the amount of carbon eliminated by the kidneys, in combination with nitrogen, is greater if excreted in the form of ammonium urate, as in birds, than in that of urea, as in mammals, obviously an advantage, since the excretory work of the respiratory organs is relieved to a corresponding extent. That the production of uric acid is due to imperfect oxidation appears, also, from what one daily observes in cases of gravel and gout diseases, in which the characteristic accumulation of uric acid or urate of sodium is without doubt, due to either albuminous food being continually taken in excess, or to the imperfect combustion of the albumen of ordinary diet, or of that resulting from the disintegration of the tissues. As in all probability albumen, whether derived from food or tissue, in being transformed into carbonic acid and urea, passes through a uric acid stage, just as starch passes through the stage of sugar, it follows that, if oxidation be arrested at a certain stage, uric acid, or urates, will accumulate in the system, and give rise to gravel or gout. An attack of gout being, chemically, a sudden oxidation of sodium urate into urea and carbonic acid, enabling the system, thereby, to rid itself of at least the mechanical effects of the disease, the best preventive to such an attack is to eat as little food of any kind, and breathe as much fresh air as possible.<sup>2</sup> The good effect of diet, accompanied with active exercise in the open air, horseback riding, etc., to increase the respiration, and the taking of alkalies and iron, to promote oxidation indirectly, experienced by those who are habitually high livers, and subject to gout, etc., is too well known to need further comment.

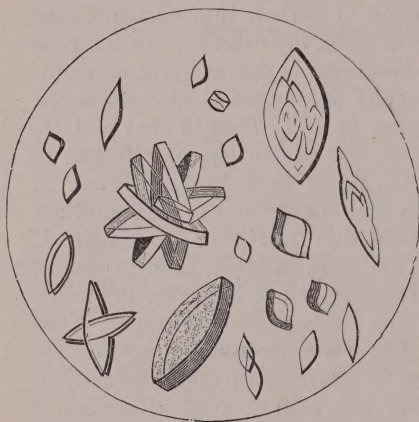
<sup>1</sup> For the heat developed in the production of CO being  $\frac{3}{4}$  that of  $CO_2 = 1$ , that developed in the production of  $C_2O_2$  equals  $1\frac{1}{2}$  that of  $CO_2$ .

<sup>2</sup> Bence Jones, op. cit., p. 126.



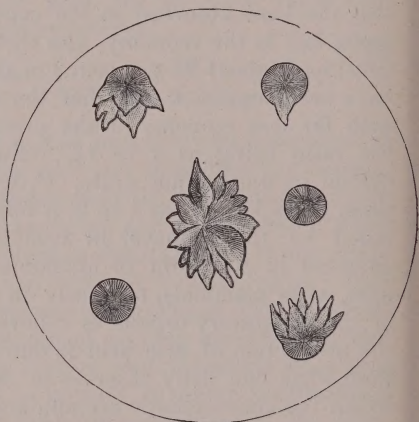
That uric acid, like urea, is derived almost entirely from the nitrogenous food, appears from the amount of it excreted being dependent upon the kind of food taken, rising to over thirty-two grains in twenty-four hours on a full meat diet, sinking to about three grains during abstinence, in the latter case the body supplying the nitrogenous food. Uric acid appears to be very generally present when active changes are taking place, being found in the spleen pulp, in the lungs, liver, pancreas, brain, and muscles. As already mentioned, the acidity of the urine is indirectly due to uric acid through its combining with the sodium of the basic phosphate, and so reducing the latter to the acid phosphate, upon which the acidity of the urine directly depends. Uric acid existing in the urine in the form of urates, usually as a brownish, yellowish, powdery substance, ammonium or sodium urate (Fig. 264),

FIG. 264.



Uric acid, deposited from urine. (DALTON.)

FIG. 265.



Sodium urate from urinary deposit. (DALTON.)

may be readily obtained by the decomposition of the same. Thus, if nitric or hydrochloric acid be added to freshly filtered urine in the proportion of about two per cent. by volume, and the mixture be allowed to remain at rest, within twenty-four hours uric acid will be deposited as thin crystals on the sides of the vessel. These crystals (Fig. 265) are usually transparent, yellowish, rhombic plates, with the angles rounded off, and are frequently collected together in rosette, star-like clusters and spheroidal masses. If uric acid be boiled with nitric acid it dissolves with a yellow color, and with an abundant liberation of gas bubbles. If the solution be now evaporated a brilliant red stain is left, which, by the addition of aqua ammonia, becomes purple. The presence of uric acid and urates can be readily determined by this procedure, which is usually known as the murexide test. It has already been mentioned that kreatinin ( $C_4H_7N_3O$ ) (Fig. 266), usually found in small quantities in the urine—about fifteen grains being excreted daily—is probably not derived from the kreatin ( $C_4H_9N_3O_2$ ), (Fig. 267) of the muscle, but, rather, from that of food, probably by dehydration, and may be regarded, chemically, as imperfectly oxidized

albumen, intermediate between the latter and urea, the disintegration of food or tissue albumen leading through kreatin, kreatinin, uranin, guanin, allantoin, xanthin, hypoxanthin, all nitrogenous products, to uric acid, which, as we have seen, is finally transformed into urea and carbonic acid.

FIG. 266.



Kreatin, crystallized by hot water.  
(LEHMANN.)

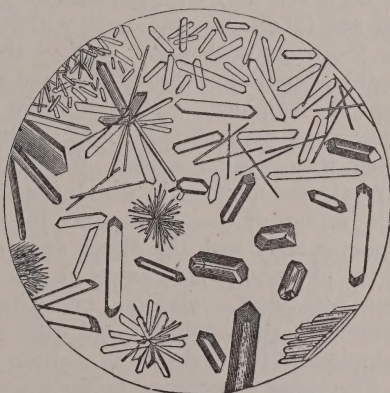
FIG. 267.



Kreatinin, crystallized from hot water.  
(LEHMANN.)

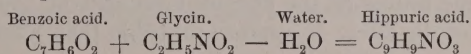
Hippuric acid,  $C_9H_9NO_3$  (Fig. 268), excreted in about the same amount as kreatinin, like the latter, is also a very imperfectly oxidized

FIG. 268.



Hippuric acid. (LANDOIS.)

nitrogenized principle. Chemically it may be regarded as being a residue of benzoic acid and glycin—that is, as formed through the conjugation of these principles with dehydration, as follows:



That hippuric acid actually arises in the body through the combination of glycin with benzoic acid appears from the fact that, if the latter be



taken internally, the amount of hippuric acid excreted is increased,<sup>1</sup> and that a benzoic acid residue naturally exists in the fodder of ruminants, which accounts for, on the above supposition, hippuric acid replacing uric acid in the urine of herbivorous animals.<sup>2</sup> Since, in jaundiced patients, and in animals in which the liver is extirpated, or the ductus communis is ligated, the benzoic acid administered passes out of the body as such, one would be led to suppose that the synthesis with glycine takes place in the liver. That hippuric acid is also formed in the kidneys appears from the fact that if arterialized blood, containing benzoic acid, be passed through the bloodvessels of a freshly excised kidney, hippuric acid will be found in the perfused blood. With reference to the plausible hypothesis, just given, of the origin of the hippuric acid in the herbivora, it should be mentioned, however, that it is found in the urine of man when on an animal diet, though in less quantity than when on a vegetable or mixed one, and that benzoic acid is not a constituent of his food.

Indican, also known as uroxanthin,  $C_{26}H_{31}NO_{17}$ , a yellowish substance, usually present in the urine of man, and in greater quantity in that of the horse, is probably derived from indol, one of the products of pancreatic digestion; through oxidation it becomes indigo blue.

The presence of the volatile acids, phenylic,  $C_6H_5O_2$ , taurylic,  $C_{14}H_8O_2$ , and damaluric,  $C_{14}H_{13}O_4$ , appears to give rise to the odor of the urine.

In addition to its organic constituents, amounting to about 550 grains in twenty-four hours, the urine contains, as may be seen from Table LXXI., a number of inorganic saline ones. These salts, amounting, in twenty-four hours, to perhaps 300 grains, though varying on a mixed diet between 140 and 378 grains, and in women between 158 and 303 grains, are taken into the body with the food, and pass out of it as such in the urine unchanged, or they are produced within the system through the oxidation of the sulphur and phosphorus, either of the food or tissue, the sulphuric and phosphoric acids so formed (a source of heat) combining with alkaline and earthy bases, the latter being in combination with weaker acids. While it is impossible, as yet, to determine exactly the manner in which the bases are related to the acids, and in the salines of the urine, since the composition of the ash corresponds almost exactly with the direct analysis of the urine, it would appear that the phosphoric acid exists in the urine in combination with sodium and potassium as alkaline, and with lime and magnesium as earthy phosphates, the sulphuric acid with sodium and potassium as alkaline sulphates, the sodium as sodium urate, phosphate, and chloride, etc. The latter constitutes by far the greater part of the inorganic constituents of the urine, as much as 250 grains and more of sodium chloride being excreted in twenty-four hours, being derived principally from the food; the amount will vary, however, considerably. Some part of the sodium chloride introduced into the system as food, appears to be the source of the hydrochloric acid of the gastric juice, and of the soda of the bile. It appears probable that, after being decom-

<sup>1</sup> Matschersky: Virchow's Archiv, 1863, S. 528.

<sup>2</sup> Meissner and Shepard: Centralblatt, 1866, Nos. 43 and 44.

posed, it is recomposed again within the system, and as such eliminated. The alkaline sulphates, amounting to 10 per cent. of the solid matter of the *uræ*, are derived from the food and the disintegration of the albuminous tissues, the greater part of the sulphur not eliminated in the feces as taurin becoming sulphuric acid, and combining with the sodium and potassium supplied by the alkaline carbonates and phosphates of the blood, about 4 grammes (60 grains) are excreted daily. The phosphoric acid of the urine is excreted principally in the form of potassium and sodium phosphate. Being readily soluble, these salts are not precipitated, and therefore do not affect the transparency of the urine. The amount of alkaline phosphates excreted, about 4 grammes (60 grains) in twenty-four hours, varies with the kind of food taken, being greater on an animal than on a vegetable diet, the former being richest in soluble phosphates, or substances yielding readily phosphoric acid. Phosphoric acid, like sulphuric, being produced in the system through oxidation of the phosphorus of the muscular and nervous tissues, the amount of alkaline phosphates excreted, like the sulphates, will depend, to a certain extent, upon the amount of tissue disintegrated. The earthy phosphates, magnesium and calcium phosphate, are usually excreted in less quantity than the alkaline phosphates, the average daily quantity of the latter being about 1 gramme (15.43 grains), or about one-fourth of the former. They are not the less important, however, from a pathological point of view, since their solubility, like the urates, depending upon the acid sodium phosphate, they will be precipitated if the latter be absent, and the urine be consequently alkaline. The earthy phosphates, while derived principally from the food, are, no doubt, formed within the system, through the decomposition of sodium chloride, calcium carbonate, etc., the bases combining with the phosphoric acid. It is in this way, probably, that the calcium carbonate of the food, or that resulting from the disintegration of osseous tissue, is eliminated as calcium phosphate in the urine. It is worthy of mention, in this connection, that on a vegetable diet the excess of alkali in the food reappears in the urine, while on an animal diet it is the excess of the earthy base that becomes conspicuous. In addition to the important organic constituents just mentioned, the urine contains, usually, traces of nitric and silicic acids, ammonia, and iron, and small quantities of nitrogen (0.8 per cent.) and carbonic acid (7 per cent.), about one-third of the latter being in a state of combination, the remaining<sup>1</sup> two-thirds free; oxygen, however, is usually absent.

Having considered the composition of the urine, it remains for us now to describe, as far as possible, the manner in which it is excreted. That the urine is excreted by the kidneys, but not elaborated by them, appears not only from what has been said of the origin of its constituents and of their accumulation after ligation of the renal arteries, extirpation of the kidneys, etc., but from the fact, also, that in certain cases referred to by Haller,<sup>2</sup> Nysten,<sup>3</sup> Burdach,<sup>4</sup> and Laycock,<sup>5</sup> in which the kidneys

<sup>1</sup> Gorup Besanez : *Physiol. Chemie*, 1862, S. 526. Bernard : *Liquides de l'Organisme*, 1869, tome i. p. 347.

<sup>2</sup> *Elementa Physiologia*, tome ii. p. 370.

<sup>4</sup> *Physiologie* (Jourdain), tome viii. p. 248.

<sup>3</sup> *Recherches de la Phys. et de Chimie*, p. 265.

<sup>5</sup> *Edin. Med. and Surg. Journal*, 1838.



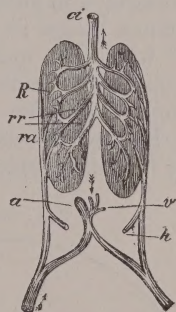
were either congenitally absent or not acting, the urine, or fluid closely resembling it at least, was vicariously excreted by the skin, pleura, peritoneum, mucous membrane of the intestinal canal, salivary, lachrymal, and mammary glands, ears, nose, etc. Such being the case, the question reduces itself to the consideration of the manner in which the different constituents of the urine are separated by the renal epithelium from the blood supplying the kidney. Now, we have seen that the urine consists of water holding in solution urea, etc., and that the kidney is made up of uriniferous tubules, each tubule consisting of two distinct portions, a tubular part and a capsular part, both lined with epithelium and supplied with bloodvessels. The bloodvessels invaginated by the capsular portion being, however, disposed in a capillary knot of far greater aggregate capacity than the branch of the renal artery from which it originates, and of the single exit vessel in which it terminates, the blood must be, therefore, retarded as it flows within the capsule, and the escape of its water much favored by such a disposition. That the function of the capsular part of the uriniferous tubule, as shown by Bowman,<sup>1</sup> is to filter, drain off the water from the blood, the urea, etc., being excreted by the tubular part and then washed out, so to speak, by the water, is confirmed by what is seen in reptiles. Thus, in the boa, uric acid, the equivalent of the urea of mammals, excreted in a solid state is only found in the tubular portion of the uriniferous tubule. The excretion of the urine will then depend essentially upon the relation of the pressure of the blood in the renal arteries, 120 to 140 mm. mercury, to that of the fluid within the tubules and ureter, 10 to 40 mm., the amount of urinary materials in the blood, and the activity of the renal epithelium. The influence of the blood pressure is shown from the fact that the excretion of urine is diminished with the lowering of the pressure of the blood whether brought about generally or locally, as by constriction of the renal artery—in fact, if the blood pressure be as low as 40 mm. the excretion of the urine ceases. On the other hand, with an elevation in the blood pressure, whether induced generally or locally, the excretion of the urine is increased. That the renal epithelium, however, exerts an excretory activity independent of the influence of the blood pressure, is shown by the experiments of Heidenhain<sup>2</sup> upon animals in which, after the flow of urine had ceased through section of the spinal cord below the medulla, sodium sulphoindigotate being injected into the veins was found, after death, in the renal epithelium or the interior of uriniferous tubules according to the length of time elapsing between the injection and killing of the animals, proving that the renal epithelium had excreted the sulphoindigotate from the blood. By varying the quantity of the salt injected and the time elapsing between the experiment and the subsequent examination, Heidenhain was able to follow step by step the salt as it passed from the blood into the cells, thence through the latter into the tubules for some little distance. There being no fluid passing along the uriniferous tubules to wash away the sulphoindigotate, the latter remained about where it had been excreted. Not a trace of the salt injected could be found in the epithelium or within

<sup>1</sup> *Op. cit.*

<sup>2</sup> Hermann: *Physiologie*, Funfter Band, Erster Theil, S. 345.

the capsular portion of the tubule, the cells excreting the sodium sulphoindigotate being of the kind described by Heidenhain as rod-shaped, more especially found in the intercanalary portion of the uriniferous tubule. It was also shown by these experiments, as might have been expected, that there was a limit to the excreting capacity of the renal epithelium, the excretion of a second quantity of sulphoindigotate injected soon after the first being very imperfect. It might be supposed that the experiments of Heidenhain with sulphoindigotate could be repeated with urea, uric acid, etc., with the view of showing that these substances are excreted by the cells lining the tubular and not by those lining the capsular portion of the tubule. Inasmuch, however, as the injection of urea, etc., gives rise to a copious flow of urine, even after section of the spinal cord below the medulla, which is not the case with the sulphoindigotate, the urea will be washed along the tubules as fast as it is excreted, which makes it impossible, therefore, to say by what part of the renal epithelium it has been excreted. It is well known, however, that in birds, reptiles, and fishes, branches from the mesenteric, femoral veins, etc., pass to the kidneys (Fig. 269), and after ramifying through the latter converge and finally terminate in the vena cava, the veins being known collectively as the renal portal system, or the system of Jacobson,<sup>1</sup> after their discoverer. The blood flows through the kidneys in these animals, therefore, very much as it does through the liver in man. Now the branches of this renal portal system, together with the efferent vessels from the glomeruli, constitute the capillary plexus surrounding the tubular portion of the uriniferous tubules, the glomeruli themselves, however, being supplied exclusively by branches of the renal artery. It is obvious, therefore, that if the renal artery be ligated the blood will be entirely cut off from the glomerulus, while that supplying the remaining portion of the uriniferous tubule will be unaffected. Such being the case, it follows that if urea still appears in the urine after ligation of the renal arteries, it must be excreted by the epithelium of the tubular and not by that of the capsular portion of the uriniferous tubule. These theoretical considerations are fully borne out by the experiments of Nussbaum,<sup>2</sup> who has shown that while sugar, peptones, and albumen are excreted by the glomeruli, these substances not appearing in the urine after ligation of the renal arteries, urea is excreted by some part of the remaining portion of the tubule, urea, when injected into the blood, giving rise to a flow of urine even after ligation of the arteries. The urine, like the bile, is excreted continuously, and while the flow may be increased or diminished, it never absolutely ceases in health for any length of time. The urine trickling through the mouth of the uriniferous tubules into

FIG. 269.



*ci.* Vena cava. *R.* Kidneys. *rr.* Vena revehens. *ra* Vena advehens. *a.* Vena epigastrica. *h.* Vena hypogastrica. *i.* Vena ischiada. (GAGENBAUR.)

<sup>1</sup> De systemate venoso peculiari in penultis animalibus observatio. Copenhagen, 1821.

<sup>2</sup> Pflüger's Archiv, 1877, xvi. S. 139; 1878, xvii. S. 580.



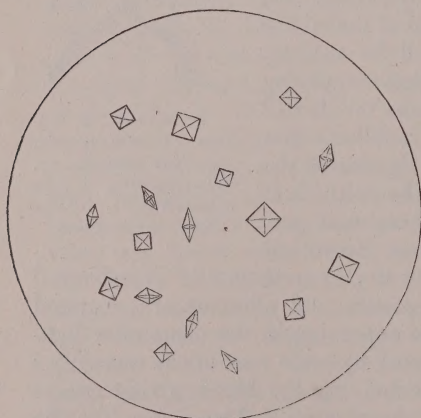
the calices, passes thence by the ureters into the bladder, its return from the latter during micturition being prevented by the obliquely disposed valvular-like orifices of the ureters.

The bladder is a musculo-membranous sac, the muscular fibres, chiefly of the involuntary character, being disposed in a longitudinal and circular manner, the former constituting the detrusor, the latter the sphincter vesicæ, by the contraction of which the urine is either expelled or retained within the bladder. Micturition appears to be brought about essentially as follows:

During the intervals in which the urine is not voided the sphincter vesicæ is in a state of tonic contraction; if, however, the urine be retained for some time the contraction of the sphincter alone is insufficient to resist the outflow, and the action of the adjacent muscles is called upon to assist it. The disposition to urinate after a time becoming very great a few drops of urine pass into the urethra, the impression so produced then calls into play the action of the detrusor and ejaculator urinæ, the sphincter being simultaneously relaxed, and the bladder is emptied. Ordinarily the voiding or the retaining of the urine is a voluntary act, but that the urine can be voided at regular intervals independent of the will is shown by the regularity with which the action is performed in animals in which the spinal cord has been divided, and in human beings in which it has been injured. The mechanism by means of which the muscular contractions are brought about in response to stimuli, the result of which is the voiding of the urine, will be better appreciated after the subject of reflex action has been considered.

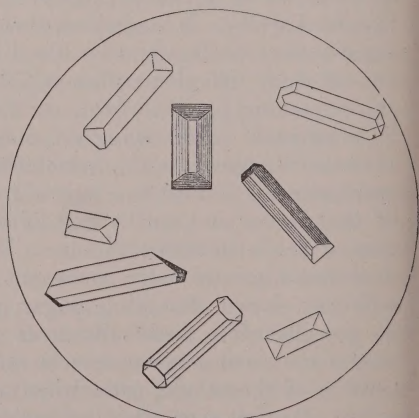
Finally, in concluding our account of the urine, the changes produced by standing may here be briefly alluded to. The urine when first

FIG. 270.



Calcium oxalate. Deposited from healthy urine, during the acid fermentation. (DALTON.)

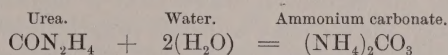
FIG. 271.



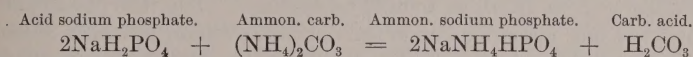
Ammonium magnesium phosphate. Deposited from healthy urine, during alkaline fermentation. (DALTON.)

passed, it will be remembered is acid, the acidity being due to the acid phosphate of sodium. Within about twelve or twenty-four hours after being passed, however, free acid makes its appearance, lactic acid being that

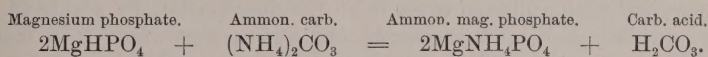
usually developed, probably from some of the organic principles of the urine by the fermentative action of fungi, and perhaps of the mucus usually present in small quantities in the urine; oxalic acid is also frequently produced, probably in the same manner, and in decomposing the salts of lime give rise to the formation of crystals of oxalate of calcium (Fig. 270). After a few days this acid fermentation ceases, through the conversion of urea by the addition of water into carbonate of ammonium, the change being brought about by the development of the micrococcus ureæ, one of the simplest of living beings, as follows :



and the neutralization of the acid sodium phosphate by the ammonium carbonate, as shown by the following reaction :



the urine becomes alkaline. With the alkalinity of the urine, the earthy phosphates being only soluble in acid fluids, are precipitated, and in combining with the ammonia give rise to the formation of the triple phosphate or ammonium magnesium phosphate (Fig. 271), as follows :



As decomposition goes on, the ammonium carbonate, after saturating the elements with which it is capable of uniting, is given off free, giving rise to the ammoniacal odor of the urine, and this continues until all of the urea has disappeared.



## CHAPTER XXXVI.

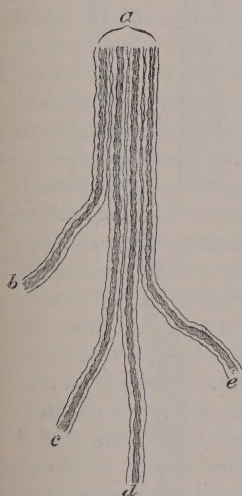
### STRUCTURE OF THE NERVOUS SYSTEM.

IN describing the manner in which food is digested, absorbed, and circulated through the economy as blood, supplying the material for the repair of the tissues and the production of heat and force; of the absorption of oxygen, and exhalation of carbonic acid, water, urea, etc., the influence exerted by the nervous system upon these processes has only been alluded to, if at all, in an incidental manner. That the phenomenon of nutrition is not dependent upon the nervous system, however much it may be influenced by the latter, is shown from the fact that the nutrition of the lower animals, in which the nervous system is but little developed, and of plants, in which, with but few exceptions, so far as is known, it is altogether absent, does not differ from the higher forms of animal life. Indeed, the essential difference between the nutrition of plants, as compared with animals, consists of the deoxidation by plants of the water, carbonic acid, and ammonia constituting their food into starch, sugar, fats, albumen, and the storing up of force, and the oxidation by animals of the latter substances constituting their food into carbonic acid, water, and ammonia, and the expenditure of force. But while such a broad distinction exists between plants and animals, as compared, on the whole, nevertheless, it must not be lost sight of that oxidations, analytical processes, are going on in the economy of plants incidental to the elaboration and circulation of the sap, the production of heat, in budding, flowering, etc., and deoxidations, synthetical processes, in the economy of animals. Indeed, as has already been mentioned, no sharp line of demarcation can be drawn between vegetable and animal life. While nutrition is not actually dependent upon the nervous system therefore, nevertheless every one is, ~~however~~, conscious of the extent to which it influences nutritive processes. The sudden manner in which digestion is brought to a stop by a piece of bad news, of the weakness of the heart induced by nervous shock, of the sudden blush or pallor due to emotion, are familiar illustrations. The flow of the secretions into the alimentary canal in response to food, the rhythmical action of the heart and lungs, though unconsciously brought about, are due equally to the action of the nervous system. The influence of the nervous system upon nutrition has often been compared to that exercised by the rider upon the movements of a horse, the force being put forth by the latter, but controlled by the bit and spur. Man, like other animals, is, however, something more than a mere nutritive machine, becoming conscious, through his nervous system, of an external world. Impressions made upon sensory nerves by heat, light, sound, etc., when conveyed to the sensorium, give rise there to sensations out of which are developed in still higher centres, emotions, desires, ideas,

while through the influence exerted by the motor nerves in the reverse direction upon the muscles the mandates of the will are obeyed. In a word, it is by means of the nervous system that the various nutritive processes that we have studied are brought into relation with each other—are coördinated—that we feel, think, will.

The nervous system, or the apparatus by which the different portions of the body are brought into such intimate sympathy, by which one sees, hears, thinks, wills, consists, structurally, of fibres and cells, the former being found in all parts of the nervous system, the latter confined, in a great measure, however, to the cerebro-spinal axis and ganglia. The fibres are principally of two kinds, the white tubular medullated, dark bordered, and the gray, pale non-medullated; the latter, however, only differ from the former, as we shall see, in not having the white substance of Schwann, and are much less abundant than the medullated kind, being found principally in the sympathetic, though, also, to a considerable extent, in the cerebro-spinal nerves. The white medullated nerve fibres constitute the white parts of the brain, spinal cord, and the cerebro-spinal nerves. If one of the latter be examined, the median nerve, for example, it will be found to consist of bundles or funiculi of ultimate nerve fibres (Fig. 272), supported (Fig. 273) by a framework of connective tissue, the epineurium *ep*,

FIG. 272.



Division of a nerve, showing portion of nervous trunk (*a*), funiculus, and the separation of its filaments (*b*, *c*, *d*, *e*). (DALTON.)

FIG. 273.



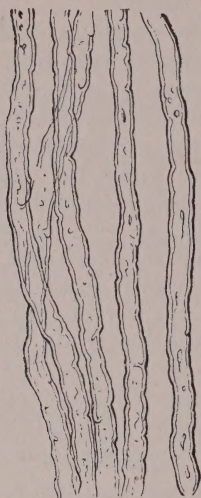
Transverse section of part of the median nerve. *ep*. Epineurium. *pe*. Perineurium. *ed*. Endoneurium. (After EICHHORST.) *a*, *a*, Funiculus. (LANDOIS.)

each of the bundles being surrounded by its special sheath of connective tissue, the perineurium *pe*, the ultimate nerve fibres, varying in diameter from the  $\frac{1}{12000}$ th to the  $\frac{1}{1500}$ th of an inch, of which the bundle or funiculus (Fig. 272, *a*) consists, being separated from each



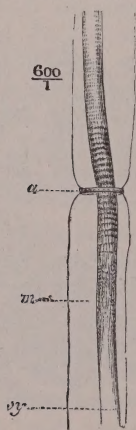
other by a more or less homogeneous substance, containing connective tissue, capillaries, etc.—the endoneurium *ed*. The ultimate nerve

FIG. 274.



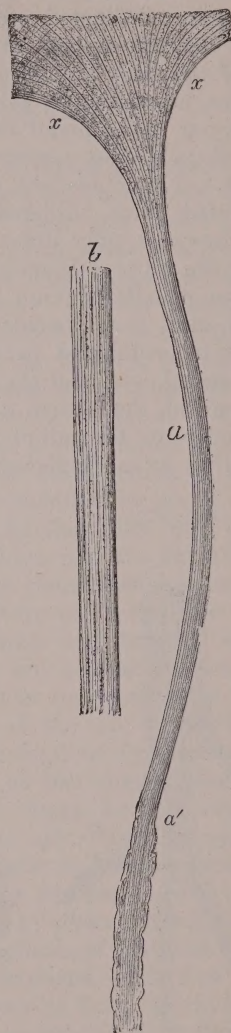
White or medullated nerve fibres, showing the sinuous outline and double contour. (After BIDDER and VOLKMANN.)

FIG. 276.



Nerve fibre from the sciatic nerve of the rabbit after the action of nitrate of silver. *a*. Ring formed by thickened membrane of Schwann. *m*. White substance of Schwann rendered transparent by glycerine. *cy*. Axis-cylinder, which just above and below the level of the annular constriction presents the striae of Frommann. (CARPENTER.)

FIG. 275.



*a*. Axis-cylinder showing its fibrillar structure; at the upper part *x*, it is seen to arise from a ganglion cell only partially represented, and to become incrustrated by a medullary sheath at *a'*. *b*. Naked axis-cylinder, from the dorsal region of the spinal cord of the ox. The medullary sheath has been removed. (CARPENTER.)

fibres, when perfectly fresh (Fig. 274), appear as transparent, clear, sinuous, double contoured, beaded, or varicose, highly refractive threads;

after exposure, however, to the action of air or water, through a process of coagulation, possibly, the ultimate nerve fibre is seen to consist of three distinct parts, a central axis, an intermediate white substance, and an external tubular sheath. The central axis, or axis-cylinder, with a diameter of about one-fourth that of the nerve fibre itself, is a pale, homogeneous, or finely granular, usually cylindrical cord, and, though soft and delicate, is, to a certain extent, elastic. In its intricate structure the axis-cylinder is fibrillar in character, the fibres being disposed longitudinally (Fig. 275); transverse striæ can, however, be also shown by appropriate treatment with silver nitrate (Fig. 276). As a general rule, the axis-cylinder cannot be distinguished in the natural condition of the nerve, owing to its refracting light in the same manner as the intermediate white substance, nor after coagulation, usually on account of the opacity developed; if the nerve fibre, however, be treated with strong acetic acid, the divided ends retracting, the protruding axis-cylinder will present the appearance just described. The axis-cylinder, further, by staining with carmine and gold chloride, can be readily distinguished in sections from the intermediate surrounding white substance. The axis-cylinder, chemically, appears to be albuminous in character; it is insoluble in water, alcohol, and ether, but soluble in a boiling solution of sodium hydrate. Through the action of concentrated acetic acid it becomes pale and swollen. From the fact of the axis-cylinder being the only constant portion of the ultimate nerve fibre, the intermediate white substance and external sheath being absent at the origin (Fig 275, *a*) and termination of the latter, there can be no doubt that it is the most important, indeed, the essential, portion, functionally, of the nerve fibre, the remaining portions having accessory functions, as will be explained presently.

The intermediate portion of the nerve fibre—that is, the part immediately surrounding the axis-cylinder, commonly known as the white substance of Schwann, but also as the medullary sheath or myelin, consists of a transparent highly refractive oleaginous material, and to which the white glistening aspect of the nerve fibre is due. The characteristic double contour, the two parallel lines on each border of the ultimate nerve fibre, indicates the external and internal limits of the intermediate layer, or white substance of Schwann. Owing to the fact of the latter becoming swollen through the imbibition of water, and exuding from the divided ends of the nerve in the so-called myelin forms, and from the after obscurity arising through the changes induced in these forms by water, and which extend into the fibre, it is more advantageous to study the white substance of Schwann by hardening and staining. Thus, when treated with perosmic acid, the white substance of Schwann becomes blackened, the axis-cylinder, however, remaining clear. If a transverse section of the nerve fibre be examined when so treated, it will be seen to consist of two concentric zones, an inner clear one, the axis-cylinder, an outer dark one, the white substance of Schwann. The white substance of Schwann appears to serve both as a protective envelope to the axis-cylinder, and as an insulator, so to speak, of the latter, so that the nerve force in its transmission



may not be diffused. The external investing portion of the nerve fibre, or the neurilemma, also known as the sheath of Schwann, the limiting membrane of Valentin, the primitive sheath or tubular membrane, a colorless transparent, almost homogeneous membrane, somewhat elastic, bears to the nerve fibre in its general properties very much the same relation that sarcolemma does to muscular fibre, and serves, without doubt, as a protective covering to the white substance of Schwann, and the axis-cylinder enclosed by the former. Although, as already mentioned, in a perfectly fresh nerve the neurilemma cannot be distinguished from the remaining white substance of Schwann, and the axis-cylinder of which the ultimate nerve fibre consists, it can be demonstrated by treating the nerve with fuming nitric acid, and then with caustic potash, the axis-cylinder being dissolved, and the fatty matters being discharged, the neurilemma remains as an empty tubular, swollen, turgid, yellow membrane, or the neurilemma can be isolated by treating the nerve with cold caustic soda, and then boiling for a moment in the same fluid. At regular intervals, along the neurilemma, may be observed indentations, the so-called constrictions, or nodes of Ranvier. At these nodes the white substance of Schwann, or medullary sheath, is indented to such an extent that the neurilemma or sheath of Schwann, comes in contact with the axis-cylinder. From the fact that a substance like picro-carmin diffuses into the axis-cylinder only at the nodes, but not into the whole substance, it is possible that it is at such points that nutritive material finds its way into the axis-cylinder and effete matter a way out. Each interannular segment of that part of the nerve fibre below the nodes exhibits when stretched oblique lines running across the white substance, and known as the incessures of Lütken. Corpuscles may also be seen at intervals between the neurilemma and the white substance of Schwann. Finally the nerve sheaths are supplied with special nerve fibres, the *nervi nervorum* to which their sensibility is due.

Non-medullated nerve fibres differ from the medullated ones in not having the white substance of Schwann, presenting a grayish, semi-transparent appearance instead of the white glistening appearance of the medullated ones. The nerve fibres of the invertebrata are exclusively of the non-medullated variety; in those of the vertebrates, however, non-medullated fibres are often found mixed with medullated ones; they are very abundant in the sympathetic, and constitute for example solely, the fibres of which the olfactory nerve consists. As, however, the medullated nerve fibres, as already mentioned, lose their white substance of Schwann, becoming, therefore, non-medullated at their origin or termination in the gray matter of the brain and spinal cord, or in sensory organs or muscles, the distinction between the two kinds of nerve fibres is not a very essential one. In addition to the medullated and non-medullated nerve fibres described there are also found in the nervous system entirely another kind of nerve fibres, indeed differing so from those just described as to have been held by competent histologists to be a variety of connective rather than nervous tissue. Such are the gelatinous nerve fibres or fibres of

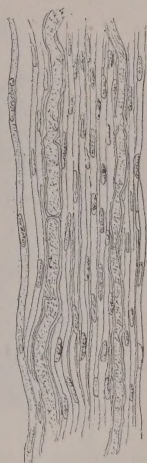
Remak, pale, flattened, granular, gray fibres, presenting well-marked, longitudinal, oval nuclei (Fig. 277), the presence of the latter giving rise to the name of nucleated nerve fibres. The gelatinous nerves-fibres are chiefly found in the sympathetic, and particularly in such portions of it influencing the involuntary muscular fibres. They have a diameter of about the  $\frac{1}{8000}$ th of an inch, and while rendered pale by the action of acetic acid, do not swell up to anything like the extent that connective tissue does under similar circumstances. Inasmuch as up to the fifth month of intrauterine life the nerves generally have essentially the same structure as the so-called gelatinous fibres of the adult, and as during the regeneration of nerves after injury or division the new elements pass in their development through a transitory stage comparable in structure to that of the gelatinous fibres, the latter may be regarded perhaps, morphologically, as undeveloped medullated or non-medullated fibres.

Neither in their course as nerve cords, nor through the white part of the nervous axis are the nerve fibres ever observed uniting or anastomosing nor dividing into branches, except at their peripheral termination. Though the nerve fibres may exist in great numbers, bound up as a nerve cord, nevertheless, like the threads in a skein of silk, they maintain their individual distinctness from their origin to their termination. When an anastomosis of nerve trunks apparently exists, it is due in reality to the nerve fibres of which the trunks consist, simply crossing over each other, the fibres from one trunk running in opposition to those of the other, each nerve fibre, however, preserving its own individual action. As the nerve fibres can be traced on the one hand into the cells of the gray matter of the nervous system, and, on the other, into muscles, glands, and sensory organs, let us consider them now in these relations.

The nerve cells (Fig. 278), constituting the most important part of the gray matter of the nervous system, are usually rounded bodies, though often of very irregular outline, and consist of a soft, nearly transparent, granular albuminous matter, with a distinct nucleus and nucleolus, and contain often, in addition, pigment of a yellowish brownish hue. The nerve cells vary very considerably in size. Thus, in the posterior horn of the gray matter of the cord, they are often as small as the  $\frac{1}{2500}$ th of an inch to the  $\frac{1}{200}$ th of an inch in diameter; whereas, in the anterior horn of the cord, they may be as large as the  $\frac{1}{200}$ th of an inch. The nerve cells are especially characterized by the manner in which the body of the cell is prolonged into one or more processes, giving rise to the name of unipolar, bipolar, multipolar, and apolar cells, where such processes are absent altogether.

As examples of unipolar cells may be mentioned those in the Gasserian and spinal ganglion, and of multipolar cells, those of the gray matter

FIG. 277.

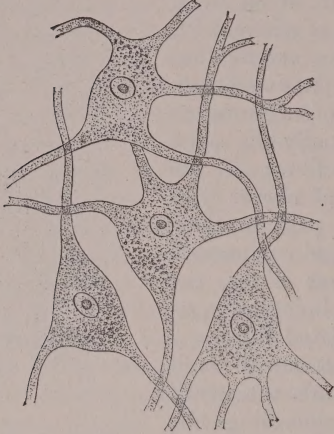


Fibres of Remak; magnified 300 diameters. With the gelatinous fibres, are seen two of the ordinary, dark bordered nerve fibres. (ROBIN.)



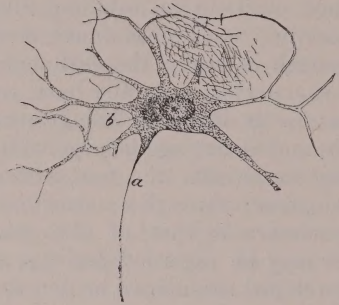
of the brain and spinal cord. Inasmuch, however, as the axis-cylinder, in many instances at least (Fig. 279), has been shown to be continuous with such processes, it is very questionable as to whether any such absolute distinction exists in the body as indicated by the terms unipolar,

FIG. 278.



Nerve cells, from the anterior horn of gray substance of the spinal cord. (DALTON.)

FIG. 279.

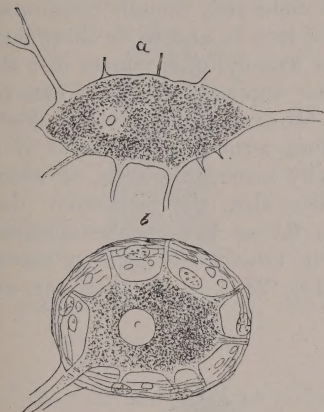


Ramified nerve cell from anterior cornu of spinal cord (man). *a.* Axis-cylinder process. *b.* Clump of pigment granules. Above the cell is seen part of the network of fibrils mentioned in the text. (GERLACH.)

apolar, etc., the distinction observed in this respect between nerve cells being very possibly due to the fact that, usually, in histological investigations, one or more of the axis-cylinders becomes separated from the body of the cell in which they are the prolongations. In other words, that the axis-cylinder of the nerve fibre is essentially a portion of the body of the nerve cell (Fig. 275), finely drawn out like a wire, the latter portion, as we have seen, being protected by a neurilemma, and insulated by the white substance of Schwann. In addition to the cells, the gray matter of the nervous system consists of scattered nuclei, usually smaller than those of the cells, and of a fine granular matter, which constitutes a kind of supporting matrix for the cells and their prolongations, or the axis-cylinders. While it cannot be said that the minute structure of the gray matter, and its relation to the axis-cylinders passing out of it, has been exactly made out as just described, nevertheless, it is highly probable that such is essentially the disposition of the same. In addition to the nerve cells just mentioned, there are other cells found in the gray matter of the ganglia, and which differ in being enclosed by a distinct sheath, or capsule (Fig. 280). The latter consists of a transparent membrane with nuclei, and appears to be continuous with the primitive sheath of the nerve fibre. The ganglia themselves, like the nerve cells, of which they are made up, are invested by a thin, but firm, envelope, continuous with the fibrous sheath of the nerves passing into them, and consist of connective tissue supporting the cells and nerve fibres. While many of the nerve fibres simply pass through the ganglia (Fig. 281), others originate in the cells of the latter, each

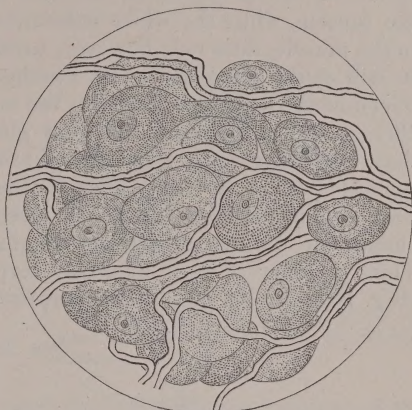
cell, according to Beale and Arnold, giving off two fibres, one of which passes out of the cell like a stalk, so to speak, while the other arises at some distance from the first, and after making several turns around the

FIG. 280.



Multipolar ganglion cells from sympathetic of man. Magnified. *a*. Freed from capsule. *b*. Enclosed within capsule. The processes of both are broken off a short distance from the cell. (MAX SCHULTZE.)

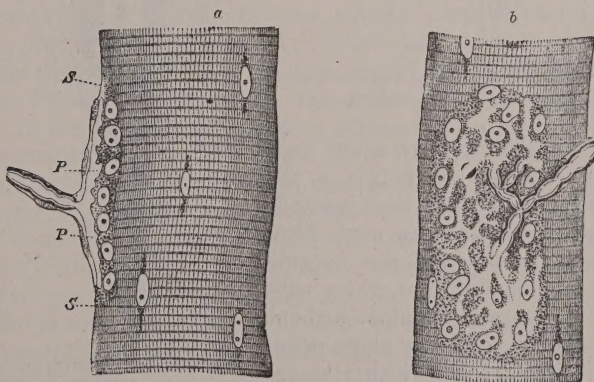
FIG. 281.



Nerve cells, intermingled with fibres; from semilunar ganglion of cat. (DALTON.)

latter, passes off in an opposite direction. Such cells are readily observed in the ganglia of frogs, but while difficult of demonstration in the ganglia of mammals, nevertheless appear to exist in the latter. If the nerve fibres be traced from their origin in the gray matter of the

FIG. 282.



Nerve-ending in muscular fibre of a lizard. (*Lacerta viridis*.) *a*. End-plate seen edgeways. *b*. From the surface. *s*, *s*. Sarcolemma. *p*, *p*. Expansion of axis-cylinder. In *b* the expansion of the axis-cylinder appears as a clear network branching from the divisions of the medullated fibre. Highly magnified. (KUHN.)

central nervous system to their peripheral distribution in muscles, glands, sensory organs, etc., it will be observed, so far as the manner in



which the nerve terminates has been made out, that the only part of the primitive nerve left at its termination is the axis-cylinder. Thus, in the termination of nerve fibres in muscles where the axis-cylinder passes into the latter, expanding into the motor plate (Fig. 282), the neurilemma of the nerve fibres becomes continuous with the sarcolemma of the muscle, while the white substance of Schwann, though continuing to the muscle, does not, however, penetrate into it, and while there may be still doubt prevailing as to whether the axis-cylinder passes into the nuclei of the cells of a gland in the manner supposed to be the case by Pflüger and others, in the salivary gland, for example, there is no doubt that, however exactly the axis-cylinder does terminate in glands, it is the only part of the nerve fibre that actually reaches the cells, of which such organs consist. Such is essentially, also, the disposition that obtains in the case of sensory organs, so far as has been established. Thus, whether it be a Pacinian corpuscle attached to sensory nerves (Fig. 283, A, B), or a tactile corpuscle (Fig. 284), as we shall see, are

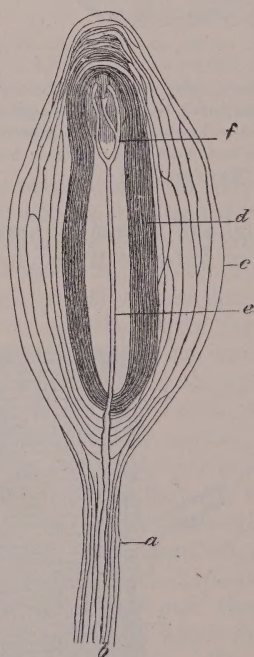
A

FIG. 283.

B



A nerve of the middle finger, with Pacinian bodies attached. Natural size. (HENLE and KOLLIKER)

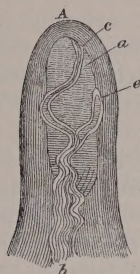


Vater's or Pacini's corpuscle. *a.* Stalk. *b.* Nerve fibre entering it. *a, d.* Connective tissue envelope. *e.* Axis-cylinder, with its end provided at *f.* (QUAIN.)

present in the skin, or a terminal bulb (Fig. 285), such as are found in the conjunctiva or tongue; in each instance will the neurilemma of the nerve fibre become continuous with the capsule enclosing such bodies, the white substance of Schwann remains without the latter, the axis-cylinder alone penetrating within. It is evident, therefore, that since the nerve fibre begins as the axis-cylinder, a prolongation of the gray matter of the cells of the central nervous system, and terminates as axis-cylinder in muscle, gland, sensory organ, etc., and as it is only the portion of the axis-cylinder intermediate between the origin and termination of the nerve fibre that

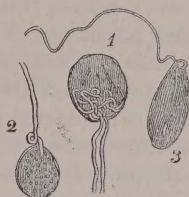
is inclosed within the white substance of Schwann and the neurilemma, that the axis-cylinder or the gray matter is the essential portion of the nerve fibre, as it is of the cell in which the former originates. In speaking

FIG. 284.



*a.* Tactile corpuscle. *b.* Nerve. (QUAIN.)

FIG. 285.



Three nerve-end bulbs from the human conjunctiva, treated with acetic acid. Magnified 300 diameters. (QUAIN.)

of the vesicular gray, or cellular, and the white fibrous portions of the nervous system, it must not be forgotten that there is but one kind of functional nervous matter, the gray, the white simply acting as a protection. While, from the fact of the nerve fibre losing its vitality if separated from the central cell, of which it is a prolongation, it follows that the nerve force, whatever its nature may be, is generated in the cells of the axis-cylinder serving for its transmission only.

If the above view be accepted, it also follows that the sympathetic must be regarded as an appendage of the cerebro-spinal system, and for which there are good reasons, as we shall see, for supposing this to be the case. This view of the nervous system, based upon the study of its structure, is further confirmed by the following considerations offered by Spencer:<sup>1</sup> That the gray matter contains more water and is more vascular than the white, and that while the cells are unprotected practically by an envelope, the axis-cylinder is inclosed by two such as we have seen, conditions favoring in the unstable gray matter destructive molecular changes and disengagement of motion, while the more stable nerve-threads are seats of molecular changes not so much destructive as isomeric in character. The matter of which the nervous system is composed consists chemically, like the remaining tissues, generally of from three-fourths to four-fifths water, the white matter containing about seventy-five per cent., the gray eighty-five per cent; the residue consists chiefly of a phosphoretted principle known as protogen, a crystalline body containing nitrogen as well as phosphorus and carbon, and which, according to some chemists, is composed of two principles, lecithin and neurin (cholin),  $C_5H_{15}NO_2$ , or lecithin and cerebrin. The gray matter contains about five per cent. the white fifteen per cent. of such phosphoretted principles. It is an interesting fact as regards lecithin,  $C_{44}H_{90}NPO_9$ , that it is the only organic principle of the body containing phosphorus. There are found

<sup>1</sup> Principles of Psychology, p. 25. Lond. 1870.



in the nervous system also cerebrin,  $C_{17}H_{33}NO_3$ , cholesterin, which has already been referred to, various extractives, and inorganic salts. Among the extractives may be mentioned lactic, formic, acetic acids, inosit, kreatin, and hypoxanthin. The inorganic principles consist principally of alkaline and earthy phosphates, sodium sulphate and chloride, iron phosphate, and traces of silica. Of the latter phosphoric acid (thirty-nine per cent.), potash (thirty-two per cent.), and soda (ten per cent.), are the most important. Beyond the mere statement of the facts, as just given, little more is positively known of the chemical composition of the nervous system, either with reference to the manner in which the ultimate chemical elements are combined or the significance of the latter.

In concluding this sketch of the nervous system, it may be mentioned here, as appropriately as elsewhere, that since there are no appreciable differences physically or chemically observed between the ultimate nerve fibres, the fact of there being, as we shall see, motor, sensory, and secretory nerves appears to depend, not upon any difference between the nerves, but upon their terminating in motor, sensory, or glandular organs respectively. That a nerve fibre will transmit an impression made upon the periphery to the centre, or from the centre to the periphery, is shown by such an experiment as that performed by Bert.<sup>1</sup> Thus the end of the tail in a young rat being denuded of integument for a length of about two inches was grafted to the back of the animal. At the end of about a week, when the ingrafted portion had become adherent, the tail was amputated at the base, the tail remaining adherent by what had been its tip. Nevertheless, at the end of six months sensibility had been unmistakably reëstablished, the caudal nerves, after the operation, transmitting impressions from the base of the tail to its tip instead of, as usually, from the tip to the base.

<sup>1</sup> La Vitalité propre des Tissues Animaux, p. 12. Paris, 1866.

## CHAPTER XXXVII.

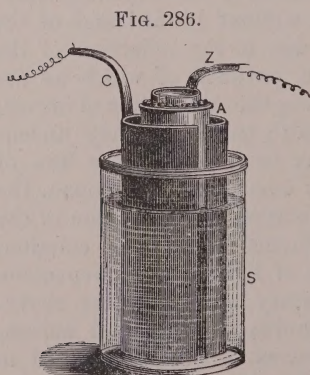
BATTERIES. OHM'S LAW. INDUCTION APPARATUS. PENDULUM. MYOGRAPH. SPRING MYOGRAPH. WHIPPE. LATENT PERIOD. VELOCITY OF NERVE FORCE, ETC.

FROM daily observation we learn that all our actions are the result of motives or stimuli. Impressions made upon the surface of the body and transmitted by nerves to the central nervous system and there giving rise to sensations, are immediately or mediately followed by actions. The impressions made may be so strong and the corresponding sensation arising so acute that action instantly follows, as in the sudden, involuntary shrinking from a source of pain or the sensation giving rise to an idea a longer or shorter time may intervene, during which period the mind has time to reflect as to the course of action, the individual being swayed by this or that idea or motive, the mind is, so to speak, in abeyance, like the ass of the schoolmen starving between the two bundles of hay, because he could not make up his mind which to eat first. Sooner or later, however, one motive becoming the strongest, voluntary action follows, or, to speak in ordinary language, the will asserts itself, the term will being simply a convenient one for expressing the fact that action is the result of the strongest motive, the result of the preceding stimulus. The sole difference between these two actions, the involuntary and voluntary, is in the interval of time elapsing between the application of the stimulus and the resulting action, and in the stimulus being that of the will or some other exciting cause, as, for example, when a cough is voluntary or due to a crumb of bread in the larynx. In addition, however, to the sensations, or ideas, arising within us due to the stimulation of nerves from without inward and of the involuntary or voluntary actions following due to the reflection of the impulses from such stimulation from within outward of which we are all conscious, there are similar actions following the stimulation of nerves, of which as long as we are in a state of health we are entirely unconscious. As illustrations of such actions may be mentioned the flow of the gastric juice in response to the stimulus exerted by food upon the nerves distributed to the stomach, of the dilatation or contraction of the bloodvessels brought about through the influence of nervous emotion, or the action of the iris under the influence of light. The phenomena of secretion like those of sensation, involuntary and voluntary movements, result from the application of a stimulus to peripheral nerves, which, being transmitted to the nervous centres, is thence reflected to the parts manifesting the phenomena. That it is by means of the nerves connecting the periphery with the nervous centre and the centre with the organs manifesting the phenomena that the latter are produced becomes at once evident if the nerves involved be destroyed,



whether by disease, injury, or experiment; sensation, voluntary movement, secretion, etc., at once disappearing as we shall see presently. The involuntary muscular contraction the result of pain, the voluntary one made in the carrying out of some of some matured plan, and the flow of a secretion, are equally illustrations of the truth of all nervous action being of this reflex character. In every instance if the phenomenon be traced to its source it will become evident that an action apparently due to an impulse generated from within and transmitted outward is in reality due to an impression first made from without and transmitted inward, and then finally reflected outward. That nervous action or force, whatever it may be, is never generated spontaneously, but must be of this reflex character, some modified preëxistent mode of motion, is self-evident, otherwise nerve force would arise out of nothing. Whatever view may be taken, however, of the origin of ideas, the nature of the will, etc., it will not affect the fact that the irritability of nerves, like that of other tissues, may be called into excitement by appropriate stimuli. While the irritability of a muscle, however, shows itself by its contraction, and that of a gland by its secretion, that of the nerve is not manifested by any ordinary visible change in itself, but as a sensation or a motion in the organ to which it is distributed. Of the different stimuli, mechanical, chemical, and electrical, available in calling into excitement the property of irritability possessed by nerves, the electrical is by far the most convenient, and since the contraction of a muscle brought about indirectly by the stimulation of the nerve supplying it, is a very striking phenomenon, the muscular contraction may be taken as an evidence and measure of nervous irritability causing it. While a sensation or a secretion might be in the same way taken as a measure of nervous irritability, as might be expected from the nature of the case it would be less convenient and less reliable.

As in the stimulation of nerves we shall usually make use of the electricity supplied by a Daniell or Bunsen battery, a brief description of the same does not appear superfluous. A single Daniell's element

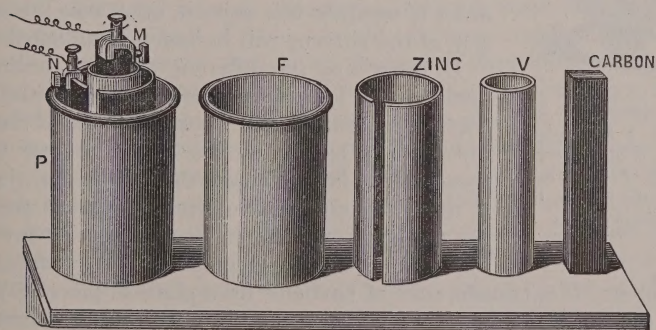


Daniell's element. (GANDOT.)

consists (Fig. 286) of a glass vessel *S*, containing a saturated solution of copper sulphate, in which is immersed a copper cylinder (*A*), open at both ends and perforated with holes, and provided with an annular shelf supporting crystals of copper sulphate to replace the solution of the same decomposed during the action of the battery. Within the copper cylinder is a thin porous vessel of unglazed earthenware, containing diluted sulphuric acid, in which is placed a cylinder of amalgamated zinc *Z*. The positive electricity generated by the action of the acid upon the zinc passing through the liquid of the battery to the copper cylinder, accumulates at the end of the wire attached by the binding screw to the latter (*C*), the wire becomes, therefore, the positive pole or electrode, though

the copper, to which it is attached from being relatively little acted upon, is called the negative or collecting plate; on the other hand, through the disturbance of the electrical equilibrium the negative electricity developed passing in the reverse direction from the copper to the zinc, accumulates at the end of the wire attached to the latter (Z), the wire becomes, therefore, the negative pole or electrode; the zinc, however, from being most acted upon, is called the positive or generating plate. As, however, the effect of the battery is due to the difference between the two currents, it is more convenient to speak as if there was but one current passing from the zinc or positive plate through the liquid of the battery to the copper or negative one, thence by the positive pole through the connecting wire back to the negative pole and so to the zinc again. Such being the disposition and action of the parts of a Daniell's element when closed; the hydrogen resulting from the action of the dilute acid upon the zinc being liberated upon the surface of the copper plate would be deposited upon the latter, causing its polarization and the action of the battery would be interfered with, were it not for the presence of the copper sulphate, which reduces it into copper and sulphuric acid, the former being deposited upon the copper plate, and the latter replacing that in the porous cup used up in acting upon the zinc; the constancy of the battery is thus insured for several hours at least, upon which its usefulness for our purpose depends. Did the hydrogen gas generated settle in minute bubbles upon the copper plate, which it otherwise would do in the absence of the solution of copper sulphate, the action of the battery would be at once interfered with, as just mentioned, by the polarization of the plate, by which is meant that the hydrogen when so deposited not only offers a resistance to the current passing from the zinc to the copper, but in generating a

FIG. 287.



Bunsen element.

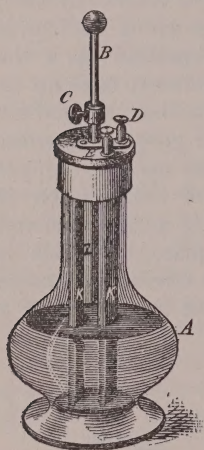
counter-current in opposition to the latter, proportionally weakens it. Further, through some of the zinc sulphate produced being attacked by the hydrogen and deposited upon the copper plate, the latter approaching the condition of the zinc plate, the difference in electrical potential would be correspondingly reduced. It need scarcely be added that if two or more elements are used in coupling, the zinc plate of one must



be connected with the copper plate of the other by means of a copper wire or strip, as in Fig. 290.

The Bunsen element, or the zinc carbon element, differing from a Grove element only in the platinum of the latter being replaced by carbon, consists (Fig. 287) of a glass or stoneware vessel (F) containing dilute sulphuric acid, in which is immersed a hollow cylinder of amalgamated zinc, within which is placed a porous vessel (V) containing ordinary nitric acid, the cylinder of carbon being placed within the latter. As in the Daniell element, the zinc constitutes the positive plate, the carbon, however, the negative one, the hydrogen developed decomposing the nitric acid, the hyponitrous acid produced passing off in fumes. A Grenet's cell, though not very constant in its action, is a convenient form of element to work with, owing to the absence of fumes. It consists (Fig. 288) of a wide-mouthed globe-shaped bottle

FIG. 288.



Grenet's element. A. The glass vessel. K K. Carbon. Z. Zinc. D, E. Binding screw for the wires. B. Rod to raise or depress the zinc in the fluid. C. Screw to fix B. (LANDOIS.)

(A), containing a mixture of dilute sulphuric acid and a saturated solution of potassium bichromate and two plates of compressed carbon (KK), which reach from the cap to nearly the bottom of the vessel, both of which are in communication with one of the binding screws in the vulcanite stopper. Through the latter passes a movable rod by which the zinc plate (Z) attached to the latter, and situated between the carbon plates and in communication with the other binding screw, can be lowered into the fluid by the rod B. Since the potassium bichromate is reduced to the sesquioxide by the hydrogen liberated through the action of the dilute acid upon the zinc, and the salt so formed deposited upon the latter, it is desirable that the bottle should be shaken up, in order to separate this deposit, otherwise the intensity of the current will be much diminished.

In describing the different batteries ordinarily made use of for physiological purposes, the electricity generated was spoken of as if flowing through the battery to the poles, as one might speak of the flow of water through pipes, just as if there was an actual electrical current present. As a matter of fact, it is needless to say with reference to the development of electricity, there

is no evidence of a transference of particles from place to place as is the case of the flow of water. It will be found, nevertheless, since the molecular changes incidental to the production of electricity are yet unknown, that such a comparison offers an extremely convenient way of presenting the essential facts, of representing to the mind in a connected way results brought about by changes, the intimate nature of which we know nothing. It might be supposed, however, at first sight, that the consideration of this subject belongs rather to the domain of physics than to physiology; but as we shall soon learn that the physiologist not only continually uses electricity as a nerve stimulus, but that

both nerve and muscle exhibit electrical currents, and offer a resistance to the passage of electricity, etc., it becomes indispensable that a brief account of the principal facts of electricity be offered, sufficient at least to enable the student to understand the terms constantly used in the description of the phenomena of general nerve physiology.

It is a well-established fact that when two metals are placed in contact, as, for example, zinc with copper or platinum, a disturbance in their electrical condition, or, as it is called by electricians, a difference in potential, ensues, the word potential being used in electrical science in the same sense as level or head of water in hydrodynamics. Now just as water at a higher level, if it finds a channel, tends to fall to a lower one until equilibrium is established; similarly if two bodies, or two parts of the same body, have a different potential—that is, are at different electrical levels, so to speak—there will be a tendency to movement from the body having a higher potential to the one with the lower until electrical equilibrium is established. The force to which this change, movement, so-called electrical current, is due, is called the electromotive force, and while its nature is unknown, it can, like any other force, be measured by the amount of work performed in the passage of a unit of electricity from one position to another, just as the force of water can be measured by the amount of work performed, as in the turning of a water-wheel, etc. Just as the force exerted in a definite time in raising a weight against gravity may be stored up indefinitely, to be set free again by the falling of the weight, and applied to the performance of mechanical work, so the force exerted in bringing up a body against another similarly electrified, and therefore offering a resistance like that of gravity, may be temporarily stored up, and with the setting free of the electricity perform work. While, therefore, the principle of electrical measurement must be the same as that of other force measurements, the particular standards used will not only differ according as statical or dynamical electricity is being considered, but as to what shall be accepted as constituting the unit of time, weight, distance, etc. As a matter of fact, with reference to statical or fractional electricity, each of two equally charged bodies is said to have a unit of electricity, if when separated by a distance of one centimetre the one will repel the other with a force which will impart in one second a velocity of one centimetre per second to one gramme of matter. As regards the galvanic or current electricity with which we have, however, more particularly at this moment to do, the unit of electricity is usually accepted as being that quantity of electricity carried in one second by a current of unit strength. The latter, however, is, of course arbitrary, but in the sense just used is one such that if a conductor one centimetre long be bent into an arc of one centimetre radius it will exert a force of one dyne, that is,  $\frac{1}{981}$  of a gramme (a gramme acquiring through gravity in one second a velocity of 981 cm. a second) on a unit magnet pole placed at the centre. But the force exerted in raising one dyne, or the  $\frac{1}{981}$  of a gramme, through one centimetre—that is, that performs technically one erg of work—will raise one such electro-magnetic unit as just described through one electro-magnetic unit of potential, or, what is the same thing, the fall of one electro-magnetic unit through one unit of

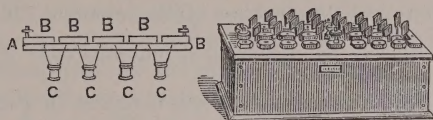


electro-magnetic potential will perform one erg of work. The latter is, therefore, in terms of a gramme or fraction of the same, metres or centimetres, and seconds, taken as the measure of the electromotive force. For convenience' sake, however, in practice a hundred millions of such absolute electro-magnetic units are taken as a unit constituting the so-called volt, and we speak, therefore, of the electromotive force of a Daniell's cell being equal to 1.079 volt. Resuming what has been just said, it may be briefly stated that the unit of electromotive force is that amount of force which sends a current of unit strength through a unit resistance, and, therefore, a unit quantity in a unit time, and this definition brings us now to a consideration of the resistance offered by the conductors in the passage of the electricity and the fixing of some standard for the same.

As the latter must be, of course, an entirely arbitrary one, the standard of resistance ultimately accepted will depend upon what is considered most convenient by electricians. As a matter of fact, at the present time, the resistance offered by a column of mercury, 104.81 cm. long, and 1 square mm. in section at  $0^{\circ}$  C., is accepted as the unit of resistance commonly known as the British Association unit, or one ohm; or, what is the same thing, the resistance offered by a wire made of an alloy of silver and platinum of definite length and thickness, offering the same resistance as the column of mercury just referred to, is accepted as the unit of resistance, or one ohm. The resistance offered by different bodies to the passage of an electrical current varies very considerably, according to the nature of the body. Metals, being the best conductors, offer the least resistance; liquids, especially those of a saline character, conduct, but not so readily as metals. Apart, however, from the conductivity of a particular substance, which is constant for that substance, the resistance offered by a conductor is directly proportional to its length, and inversely proportional to its cross-section—that is, the longer the conductor the greater the resistance, the thicker the conductor the less the resistance. In the case of a galvanic element, however, like that of a Daniell's cell, not only must the resistance offered by the conducting wires, which may be called the external resistance, be taken into consideration, but also the resistance offered by the plates and liquid within the cell, and which may be called the internal resistance. The latter is directly proportional to the distance of the plates from each other, and inversely proportional to the size of the plates—that is, the larger the plates the less the resistance, the conducting power of the liquid, of course, being assumed to be constant. In the determination of the electromotive force, resistance, etc., of nerves it will be found, as we shall see presently, that it is of great advantage to vary by known amounts the resistance offered to the passage of an electrical current. For this purpose we make use of a resistance box, which consists, essentially (Fig. 289), of a series of bobbins (C C) on which are coiled various lengths of standard insulated wire, the latter being so disposed in the box that two ends of the wire of each bobbin (C C) are connected with two brass plates (B B) fitted into the lid of the box, the resistance offered by each coil of wire being indicated in ohms on the lid of the box. Suppose, by means of the two binding

screws attached to the lid of the box, a current of electricity be sent through the coils C C, the resistance encountered will be equal to the total resistance offered by the coils. If, however, the space intervening

FIG. 289.



Resistance box. (MCGREGOR-ROBERTSON.)

between the brass plates be plugged up by tight-fitting brass plugs (Fig. 289), so that the brass plates are then connected, the current will take the route of least resistance, passing simply through the brass portion of the lid of the box, from binding screw to binding screw, without traversing the coils at all. It is obvious, therefore, that, according to the number of brass plugs that are out, will be the amount of resistance offered to the current. We have just seen that the passage of an electrical current through a galvanic circuit is due to the electromotive force developed by the element; and further, that, according to the nature of the circuit, the current meets with more or less resistance. It follows, therefore, as shown by Ohm,<sup>1</sup> first from theoretical considerations, and subsequently by experiment, that the intensity of the current—that is, the quantity of electricity which, in a unit of time, flows through a given section of the current—must be equal to the ratio of the resistance to the electromotive force. This important result, usually known now as Ohm's law, may be conveniently expressed by the equation (1)  $I = \frac{E}{R}$ , in which  $I$  represents the intensity,  $E$  the

electromotive force, and  $R$  the resistance. Ohm's law is not only a most important one from a theoretical, but also from a practical point of view, since, by means of it, galvanic batteries are so arranged as to give the greatest amount of electricity possible. From this point of view, however, it will be sufficient, for our present purpose, to illustrate Ohm's law only by such examples as will facilitate the comprehension of the methods of determining the electromotive force and resistance of nerves, etc., to be presently described.

It will be remembered that the resistance of a conductor is directly proportional to its length, and inversely proportional to its conductivity and section, if now the length, conductivity, and section be represented respectively by  $l$ ,  $c$ , and  $s$ , then the resistance  $R$  will be equal to  $\frac{l}{c \times s}$ . This value of  $R$  being substituted in equation (1) we shall

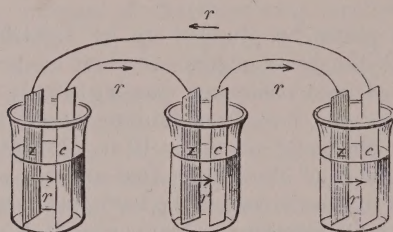
obtain  $I = \frac{E}{\frac{l}{cs}} = \frac{csE}{l}$  (2)—that is to say, the intensity of a current is

<sup>1</sup> Die galvanische Kette mathematisch bearbeitet, Berlin, 1827. Also translated in Taylor's Scientific Memoirs.



directly proportional to the section and conductivity of the conductor, but inversely proportional to its length. In the case of a galvanic element, as we have seen, the resistance to be considered is not only that of the conducting wires, but also that of the liquid and plates of the element itself. Calling the external resistance, that of the wires,  $r$ , and the internal resistance, that of the element,  $R$ , we obtain from equation (1)  $I = \frac{E}{R \times r}$  (3). Now it is obvious that if any number of similar elements are joined together, say three, as in Fig. 290, there is  $n$

FIG. 290.



Galvanic elements.

times the electromotive force, but, at the same time,  $n$  times the internal resistance, and equation (1) becomes  $I = \frac{nE}{nR \times r}$  (4). If, however, the conducting wires be of copper, and short and thick, then the external resistance  $r$ , in comparison with  $R$ , may be neglected, and equation (4) becomes  $I = \frac{nE}{nR} = \frac{E}{R}$  (5)—that is to say, when the internal resistance is great and the external is small, a battery consisting of several elements—three, in this instance—produces no greater effect than one element. Suppose, on the other hand, that the conducting wires be very long and thin, or the conductor be a bad one, as a liquid, the external resistance  $r$  offered is, under these circumstances, very great; but if now, at the same time, the internal resistance  $R$  is small, as in the thermo-electric pile, for example, the latter, or  $R$ , can be neglected in comparison with  $r$ , and equation (1) becomes  $I = \frac{nE}{r}$  (6), but as

$I = \frac{E}{R}$ , we will obtain from (6)  $I = nI$  (7)—that is to say, when the external resistance is large, and internal resistance small, the intensity within certain limits is very nearly proportional to the number of elements—that is, a battery consisting of three elements produces nearly three times the effect of one element. Instead of increasing the number of elements, let us now enlarge the plates, say  $n$ , or three times of a single element (Fig. 291), and see what effect will be obtained according to Ohm's law. The electromotive force under these circumstances will, of course, remain unchanged—that is, not increased, since it depends upon the nature of the plates and the liquid, and not upon the size of the element, just as the head or force of the

water comparable to the electromotive force is not increased as long as the level remains unchanged, however much the amount of water may be increased, for though there are  $n$  times as many regions, in this case—three, where the electromotive force acts side by side—they do not assist one another any more than the neighboring vertical columns of water in a reservoir affect the pressure on the exit pipe. Nevertheless, just as in the previous instance, in which the battery was supposed to consist of three elements, there will be a difference in the effect produced according to whether the external or internal resistance is neglected, since although the electromotive force does remain unchanged, the increase in the size of the plates must be followed by a proportional diminution in their resistance which permits a proportional quantity of electricity to pass through them. Let us first suppose that the external resistance, or  $r$ , be so much smaller than the internal or  $R$ , that it can be neglected, and that the plates have been enlarged three  $n$  times, then we have obtained from equation (1)—

$$I = \frac{E}{\frac{R}{n} + r} = \frac{E}{\frac{R + nR}{n}} = \frac{nE}{R + nr} = \frac{nE}{R} = nI \quad (8)$$

that is to say, by enlarging the plates of the element  $n$ , or three times, (Fig. 291) when the external resistance is small, the intensity is increased correspondingly. On the other hand, suppose the internal resistance, or  $R$ , is so small that it can be neglected, then equation

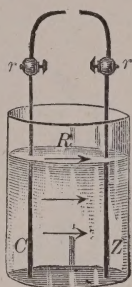
$\frac{nE}{R \times nr}$  of the above series becomes  $\frac{nE}{nr} = \frac{E}{R}$ , and since, as before,

$I = \frac{E}{R}$ , we finally obtain from equation (1)  $I = I$  (9)—that is to say,

by enlarging the plates of the element  $n$ , or three times, when the internal resistance is small the intensity is scarcely increased. Resuming what has just been said, we learn by Ohm's law that if the internal resistance be small, it is of advantage to increase the number of cells; on the other hand, if the internal resistance be large, while it is of no advantage to increase the number of cells, it is of advantage to enlarge the cell, nothing, however, being gained by enlarging the cell if the internal resistance be small. It need hardly be added that while the intensity or quantity of electricity flowing through the circuit in a given time remains the same, the density of the current may, however, vary, the latter being inversely as the cross section of the conductor—that is, the less the cross section, the greater the intensity.

As in the stimulation of the nerves by electricity derived from the batteries just described, we ordinarily make use of the induction apparatus of Du Bois-Reymond<sup>1</sup> (made for the author by Elliott, of London), a

FIG. 291.



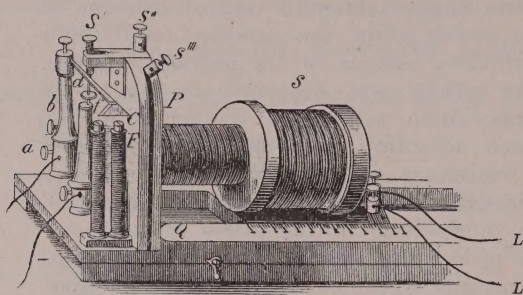
Galvanic element.

<sup>1</sup> Untersuchungen über thierische Electricität, Zweiter Band, S. 393. Berlin, 1849.



brief description of that most useful instrument in this connection appears appropriate. As its name implies, it is an apparatus (Fig. 292) by means of which an induced current can be applied to a nerve,

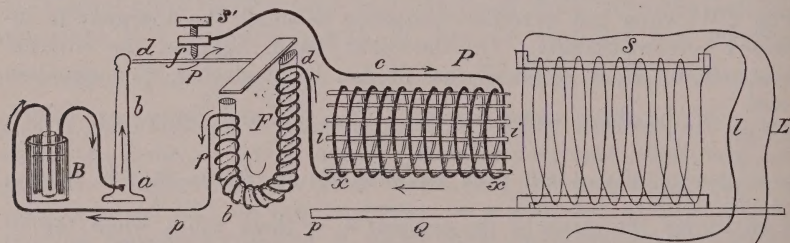
FIG. 292.



Du Bois-Reymond's induction apparatus. (LANDOIS.)

and in order that the strength of the current may be varied at pleasure, the secondary coil *S*, to which the electrodes *LL* are attached, is placed upon a graduated slide (*Q*), so that it can be made to approach or recede from the primary coil *P*, as near or far as desired. The

FIG. 293.

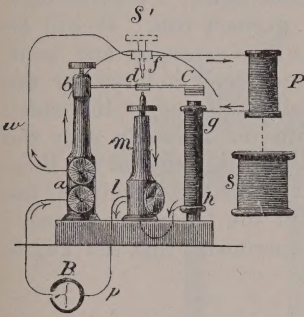


Schema of Du Bois-Reymond's induction apparatus. (LANDOIS.)

current from the battery (*B*, Figs. 293 and 294), a Daniell or Bunsen, entering the apparatus at the binding screw *a*, passes up the pillar *b* and through the German silver spring *d*, then through the primary coil *P*, and the coil *F*, returning to the battery by the binding screw *h*. As the current enters the primary coil *P*, an induced closing or making current is for the moment developed in the secondary coil *S*, and in an opposite direction to the primary current. During the passage of the current, however, through the coil *F*, the iron core within the latter becoming magnetized, the spring *d* is pulled down from the screw *f*, the result of which is that the current is short-circuited, and returns directly back to the battery through the pillar *m* and binding screw *h* without, therefore, passing through the primary coil, the result of such short-circuiting being that at the moment of the diverting of the current from the primary coil *P* there is devel-

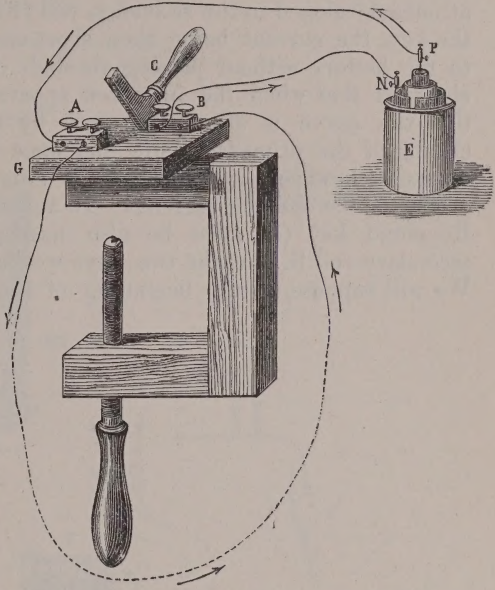
oped for a moment in the secondary coil  $S$  an induced breaking or opening current in the same direction as that of the primary current. As the iron cores within the coil  $F$  under these circumstances become demagnetized through the absence of the current, the spring  $d$  flies

FIG. 294.



Helmholtz's modification of Neef's hammer. As long as  $f$  is not in contact with  $d$ ,  $g h$  remains magnetic; thus  $f$  is attracted to  $d$ , and a secondary circuit,  $a, b, d, m$ , is formed;  $C$  then springs back again, and thus the process goes on. A new wire is introduced to connect  $a$  with  $f$ .  $B$ . Battery. (LANDOIS.)

FIG. 295.



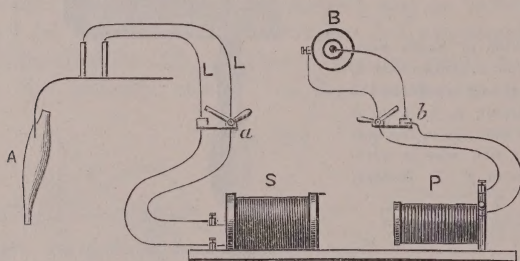
Du Bois-Reymond's key. (SANDERSON.)

up again; contact being again made with the screw  $f$ , the current passes as before through the primary coil, to be again broken with the magnetization of the core within the coil  $F$ , and to be again made with the demagnetization of the same, and so on indefinitely. The effect produced by the iron core within the primary spiral is the same as that of the primary spiral itself, since in being magnetized and demagnetized through induction by the making and breaking of the primary circuit, the core induces closing and opening currents in the secondary spiral similar to those due to the making and breaking of the current in the primary one. By applying the electrodes  $LL$  attached to the secondary coil, the nerve can therefore be stimulated by the making and breaking induced currents, which so rapidly succeed each other that the muscle is soon brought into a tetanic condition. If, however, it is desired to stimulate the nerve by a single induction shock—that is, by one closing and one opening induced current, then the wire of the battery must be attached to the binding screw  $S'$  instead of  $a$ , a Du Bois-Reymond key (Fig. 295) having also been inserted within the circuit of the primary coil, between  $B$  and  $A$ . The key being down, the current will then be short-circuited—that is, will pass directly back to the battery  $B$ , since the resistance offered by the key is less than that offered by the nerve.



With the elevation of the key, however, the current will pass through the primary coil P, developing the closing, or making induced current in the secondary coil S as before; but, as the current through the primary coil is not broken through the fall of the spring, the wire being attached in this experiment to S', there will be no opening or breaking current induced in the secondary coil. The latter is, however, at once developed in the secondary coil (Fig. 296) by simply depressing the key, the current being then short-circuited again, it returns back to the battery without passing through the primary coil. It will be observed that when the induction apparatus is so arranged and used, that the nerve is stimulated once by the current induced by the closing of the primary circuit, and once by the opening of the same. Suppose, however, it be desired to stimulate the nerve by only the closing or the opening current? To accomplish this, a second Du Bois-Reymond key (*a*) must be also inserted within the circuit of the secondary coil S, and the two keys worked in the following manner: We will suppose, at the beginning of the experiment, that the key *b*,

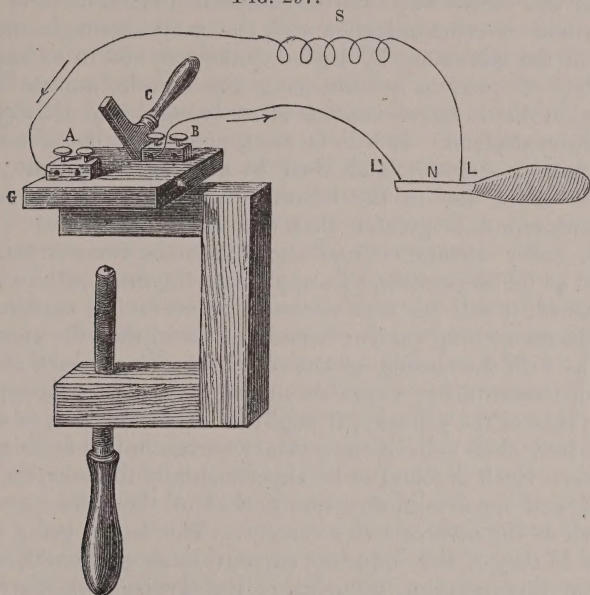
FIG. 296.



within the circuit of the primary coil P, is down, and the key *a*, within that of the secondary coil S, is up, then the elevation of the key *b*, and the passage of the current from the battery through the primary coil, there will be developed for an instant in the secondary coil an induced current, and the nerve will be stimulated by a closing or making single induction shock. The key *a* should now be depressed so that the nerve will not be stimulated by the opening or breaking of the current in the primary coil, due to the depressing of the key *b*, and the consequent short-circuiting of the current. The nerve has then been stimulated by the closing of the current only. Supposing the two keys to be both down, let us now elevate the key *b*; the secondary current developed in consequence will not influence the nerve as in the preceding experiment, since the key *a* being down, the secondary current is short-circuited. If, however, now the key *a* be elevated, and the key *b* depressed, the secondary current developed through the breaking of the primary current will be transmitted to the nerve, and the latter will be stimulated by the opening or breaking current only. Whether it be desired to stimulate the nerve by a single induction shock, or many successive ones, or by the secondary current induced through the making or breaking of the primary one, it is of advantage

always to use the key (*a*, Fig. 296) just described, not only on account of convenience, but to avoid muscular contraction due to unipolar induction, so-called, on account of the current being transmitted to the nerve by one electrode only, as is the case when the key is used, as in Fig. 297, and the key is open. While no secondary current is then

FIG. 297.



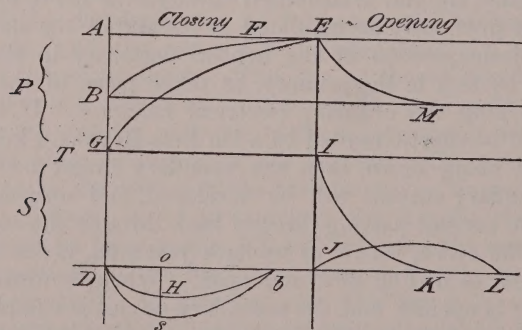
Du Bois-Reymond's key.

induced in *S* by that in the primary, the second circuit (*S*) being broken, free static electricity, however, is given off at the end of the single electrode (*L*), and transmitted through the nerve to the muscle, the electricity previously accumulated at the end of the electrode being due to the decomposition of the neutral electricity in the secondary coil, induced by that in the primary, as takes place in the prime conductor in working the ordinary electrical machine. If, however, the secondary coil be short-circuited by a Du Bois-Reymond key, as in Fig. 295, the key being down, then the secondary circuit being perfectly closed, a secondary current will be developed, and unipolar induction prevented, the current passing directly back through the coil, and none passing into the nerve, which, as we have just seen, is not the case, the key being used, as in Fig. 297, and open. When, however, the short-circuiting key is opened, and the secondary circuit is completed by the nerve intervening between the electrodes, the circuit being but imperfectly closed, unipolar induction may occur even then, as when the key is used as in Fig. 297. If, however, there be any doubt as to whether the muscular contraction be due to the stimulus exerted by the nerve excited by the secondary current, or to the unipolar induction shock—that is, the direct transmission of the static electricity through the



nerve to the muscle—it can be at once decided by simply dividing the nerve between the lower electrode and the muscle, since, if contraction then ensues, the ends of the nerves being approximated, it must be due to unipolar induction, and not to the nerve, as the division of the nerve does not interfere with the transmission of the electricity, but makes impossible that of the nerve force. It may be mentioned, in this connection, that the surest way to avoid unipolar induction is to put the upper electrode in communication with the earth through the gas or water pipe of the laboratory by a good conductor, and in so leading the free electricity off, prevent it influencing the muscle, and so effecting the contraction due to nerve excitement, as brought into activity by the secondary current alone. It will be seen, presently, that if a nerve be stimulated first by a closing and then by an induced current, that the physiological effect due to the latter, as shown by the extent of the muscular contraction, is greater than that due to the former. Now, it is desirable, under certain circumstances, that the two currents should be equalized as far as possible. To appreciate the manner in which this is accomplished, it will be first necessary, however, to explain briefly why the induced opening current is more powerful than the closing one. Inasmuch, as with the closing of the current in the primary coil, there is developed, momentarily, a current in the secondary one, opposite in direction to that of the primary, it might be suspected that, in a similar manner, the individual coils of the primary current would act inductively on each other. Such is found to be experimentally the case, the current so produced, and opposite in direction to that of the inducing current, being known as the inverse extra current. The latter, being opposite in direction to that of the inducing current, must weaken it, and it is on account of this retarding influence of the inverse extra current that the closing primary current only gradually attains its maximum intensity, as may be represented graphically (Fig. 298)<sup>1</sup> by the curve line *GE*, in which the horizontal line *T* represents the duration

FIG 298.



of the current. The corresponding closing current, induced in the secondary coil, may in the same manner be represented by the curve

<sup>1</sup> Du Bois-Reymond: *Gesammelte Abhandlungen*, Erster Band, S. 236. Leipzig, 1875.

$D G$ , only the ordinate  $o s$  must be drawn below the line  $D J$ , since the current is in the opposite direction to that inducing it. In a similar manner, at the moment of the opening of the primary current, there is developed within the primary coil a direct extra current, so called on account of it being in the same direction as the current inducing it, and therefore intensifying it. But, as there is no arrangement in the ordinary inducing apparatus by which the primary current is maintained, the direct extra current is suppressed at the opening of the primary current, the latter is therefore suddenly interrupted when at its full strength, and may be represented graphically by the perpendicular line  $E I$ , and the opening current in the secondary coil by the perpendicular  $J L$ , it being in the same direction as that in the primary, and which, having attained its maximum, suddenly falls off more gradually, as shown by the curve line  $I K$ . From the sudden manner in which the opening current developed in the secondary coil attains its maximum intensity  $J L$ , as compared with the gradual increase of the closing one  $D G$ , it becomes evident why the effect of the stimulation by the former current is greater than that by the latter. Such being the case, the induction apparatus being used as just described, let us modify the instrument a little, as done by Helmholtz,<sup>1</sup> by connecting the binding screw  $a$  (Fig. 294), by means of a wire ( $w$ ), with the binding screw  $S'$ , and lowering the silver spring ( $d$ ) away from the point of the binding screw, the current will then pass by the connecting wire directly into the primary coil  $P$  without passing first along the spring, and from the primary coil back to the battery by the coils  $g h$ ; but with the magnetization of the core within the latter the spring will be lowered, and the greater part of the current being short-circuited will then pass directly back to the battery by the spring  $d$  and pillar  $m$ , the primary current being then weakened, as represented graphically to the extent of the lines  $A B$ , the magnetization of the core within the coils  $g h$  (Fig. 294) will not be sufficient to keep the spring down, the short current will be reopened, and all the current will pass through the primary coil again. The Helmholtz modification being used, as just described, it will be observed that, as the current in the primary coil is never entirely interrupted, the direct extra current developed at the moment of the opening of the primary current within the latter will reinforce the primary current, the two currents having the same direction. The partial interruption of the primary current, and the development of the opening secondary current will, therefore, be both gradual, as shown by the curves  $E M$  and  $J L$ , respectively, which is not the case, as we have seen, when the ordinary inducing apparatus is used, since the primary current, being entirely interrupted, the direct extra current cannot make this reinforcing effect felt, the opening secondary current  $J L$ , with Helmholtz's modification, attaining then its maximum intensity, gradually, like that of the closing secondary one  $D H G$ .  $D R G$ , being diminished proportionately with  $A G$ , differs but little in its physiological effect from the latter when used as a stimulus. Finally, it will be observed that

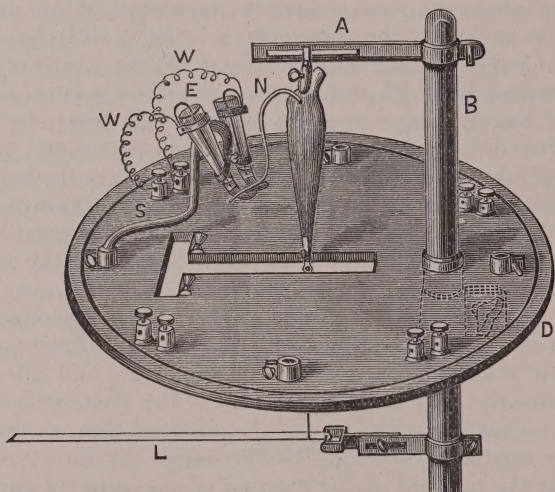
<sup>1</sup> Du Bois-Reymond, op. cit., S. 231.



the primary current never being entirely interrupted, Helmholtz's modification being used, the closing (*D H G*) and the opening (*J L*) currents are produced through the alternate strengthening and weakening of the primary current, represented by *C B* to *A* and back to *B*, due to the opening and closing of the short circuit.

That part of the sciatic nerve supplying the gastrocnemius muscle in the frog being the one that we shall make use of in our experiments, on account of its length and the readiness with which it is exposed, it may be mentioned that in preparing the nerve it should be touched as little as possible, and never seized with a pair of forceps, though it must be completely separated from the adjacent nerves. The gastrocnemius muscle, the contraction of which we take as a measure of the stimulation of the nerve, having been cut through at its insertion, the tendo Achillis must be completely freed up to its origin at the end of the femur; of the latter enough should be left so that it can be firmly clamped to the bar *A* (Fig. 299), of the upright *B*, the tibia and fibula being, however, entirely

Fig. 299.

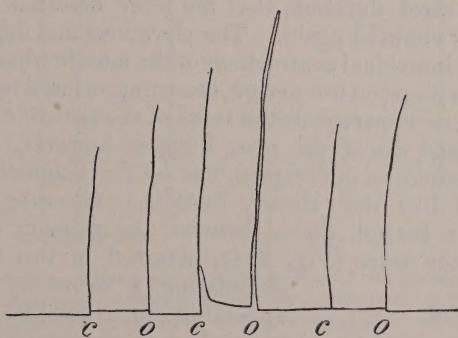


The moist chamber, with the nerve-muscle preparation, non-polarizable electrodes, electrobearer, and lever in position ready for an observation. The glass cover is not shown. (Foster.)

removed. If the nerve and muscle preparations so prepared and clamped be covered with a glass bell fitting into the rim of the disk *D*, of ebony or other hard wood through which the upright *B* passes and supports a few pieces of wet blotting paper, having been also previously placed upon the disk, the nerve and muscle will be prevented from getting dry. The disk is also provided with binding screws (*S*) for receiving the wires from the secondary coil of the induction apparatus, and from the electrodes *E* supporting the nerve *N*. The electrodes should be non-polarizable—that is, electrodes which, while transmitting the current from the secondary coil of the induction apparatus, will not generate a current by contact with the nerve. Of the different forms of non-

polarizable electrodes a convenient one is that consisting of a glass tube (Fig. 299, E), bent and plugged up at one end by a putty made of china clay and 0.75 per cent. solution of sodium chloride, and containing a saturated solution of zinc sulphate, into which is immersed to a depth of about 3 mm. a slip of thoroughly amalgamated zinc. The wire W leading to the binding screw is attached to the latter, and is usually sufficiently strong to hold up the electrodes; if not, the latter can be movably clamped to the upright, or supported as in Fig. 299, by an electrode bearer. The glass tube is often closed at its extreme point, the plug of clay being exposed only where the small orifice has been drilled. Through an opening in the disk of the moist chamber the muscle can be attached to a lever (Fig. 299, L), and its contractions made very evident by the elevation of the latter. If the point of the lever be terminated by a brush or pen, by means of the blackened cylinder already described, a graphic representation of the muscular contraction can be obtained and preserved for future reference. The lever consists of a thin slip of wood, the portion near the fulcrum being of metal and perforated or notched to receive the hook attached to the tendon of the muscle, and has usually suspended from it a scale pan containing counterpoising weights varying from between 10 to 200 grammes. The moist chamber being so attached to the recording apparatus by means of its upright that the point of the lever is brought in contact with the blackened surface of the cylinder, the latter is made to rotate for a moment so as to obtain first a base line. The nerve being now stimulated first by a closing and then by an opening shock; without Helmholtz's modification being used it will be observed from the traces obtained (Fig. 300), that the lever is elevated higher in the latter

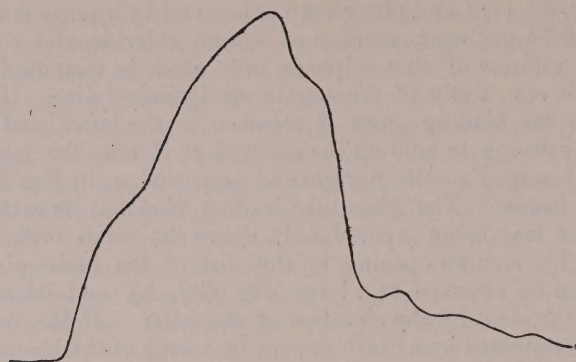
FIG. 300.



case O, than in the former C, the effect of the opening shock being greater than that of the closing for the reasons already given. The cylinder being now made to rotate rapidly, and the nerve stimulated as before, the traces obtained (Figs. 301 and 302), instead of being vertical lines will be curved ones. If now the nerve be stimulated by a series of closing and opening shocks the magnetic interrupter being used, the muscle will be brought into a tetanic condition, and the lever will be

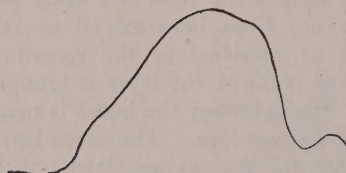


FIG. 301.



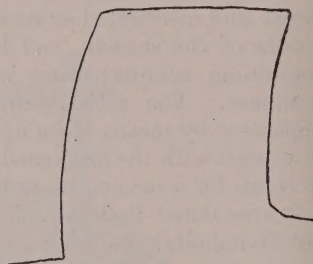
Opening shock.

FIG. 302.



Closing shock.

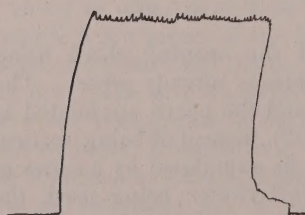
FIG. 303.



Curve of tetanus.

observed to remain elevated (Fig. 303), the interval between each shock being of short duration, that the lever descends but a little distance when it is elevated again. The elevations and depressions of the lever due to the individual contractions of the muscle when so rapidly produced, are, however, soon lost to view, becoming so fused together that they are not, therefore, apparent in the trace of the muscle curve of tetanus. The slight fall and rise of the lever become, however, quite evident if the primary current be interrupted, not by the magnetic arrangement, but by a reed like that already described, vibrating at the rate of sixteen times a second, placed between the primary coil and a key, as shown by the trace (Fig. 304), obtained in this manner. If, in

FIG. 304.

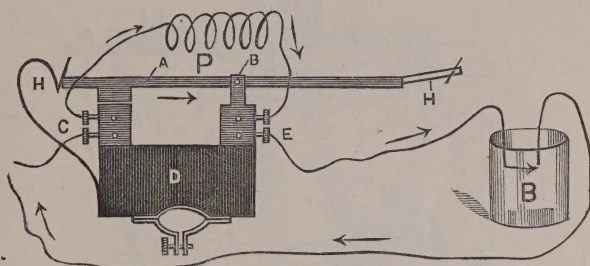


Muscle curve. Primary current interrupted sixteen times a second.

stimulating a nerve by the induction apparatus, for example, the electrodes be applied to the nerve as near as possible to the muscle, a chronographic apparatus being at the same time used, and a marking lever such as represented in Fig. 305, be substituted in the primary circuit for the key B, the moment at which the nerve is stimulated will be recorded upon the cylinder by the depression of the point of the lever (P), the velocity of the electricity being

so great that the nerve may be regarded as being stimulated at the same instant that the point of the lever is depressed, due to the elevation of the handle H, the current previously short-circuited through

FIG. 305.



The marking lever. (SANDERSON.)

C A B E, the lever being down being then thrown into the primary coil and inducing a current in the secondary coil. The marking lever A, being placed in contact with the cylinder above the pen of the chronograph B, and below that of the muscle lever c (Fig. 306), it will be

FIG. 306.

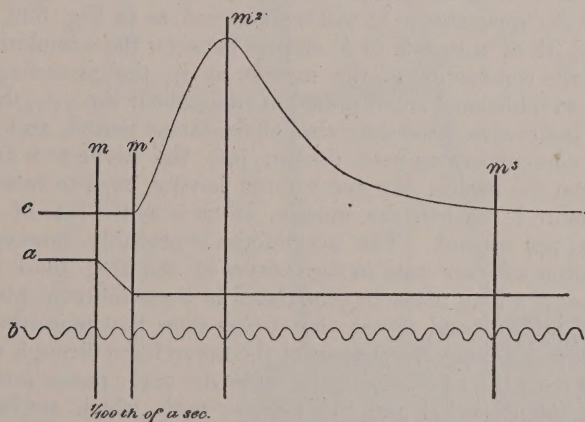


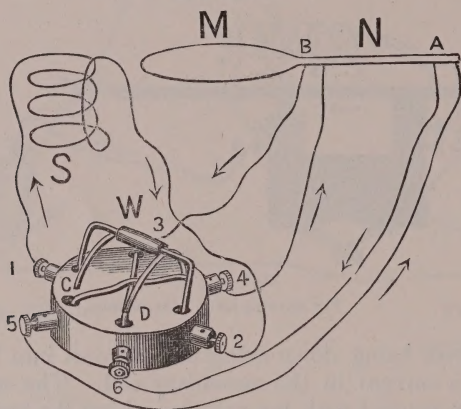
Diagram of a muscle curve as drawn on a travelling surface. c. The line described by the point of the lever connected with the muscle. a. The line described by marking lever. b. The line described by the tuning-fork. The vertical line m marks the moment of stimulation.  $m^1$ , the beginning;  $m^2$ , the maximum; and  $m^3$ , the end of the contraction of the muscle. (FOSTER.)

observed that usually the  $\frac{1}{100}$ th of a second elapses, as determined by the chronograph, between the stimulation of the nerve and the contraction of the muscle, the latent period so-called on account of the irritation being latent, not as yet actively efficient in the muscle. If the electrical currents, however, be thrown not into that part of the nerve (Fig. 307, B) in immediate contact with the muscle M, as in the preceding experiment, but at some distance from the latter, say an inch, as at A, for



example, and which can be readily done by means of the whippe (Fig. 307, W), by simply connecting the ends of the curved wires c d, with the mercury cups at 5 and 6, instead of with the cups at 3 and 4, the cur-

FIG. 307.



Whippe.

rent being then diverted without involving any other change in the disposition of the apparatus. It will be observed, as in Fig. 309, that not only the  $\frac{1}{100}$ th of a second (*a b*) elapses between the stimulation of the nerve and the contraction of the muscle, as in the preceding experiment, but an additional small period of time, about the  $\frac{1}{1100}$ th of a second (*b b*), intervenes, preceding that of the latent period, and evidently due to the current having been thrown into the nerve at a distance of an inch from the muscle, the nerve force having then to traverse that distance before it reached the muscle, which is at the rate of 91.8 feet (28 metres) per second. The nerve force is probably, however, transmitted at even a slower rate in the nerves of the frog than that just given, since, if a long nerve be stimulated in three different places, near the muscle, midway and above, the curves show that more than double the time elapses during the passage of the nerve force through the whole nerve than from the middle point to where the nerve passes into muscle.<sup>1</sup> While the latent period and the velocity with which nerve force is transmitted, can be determined in the manner just described, a more convenient and graphic method is by means of the pendulum myograph<sup>2</sup> of Fick, as modified by Helmholtz, or the spring myograph of Du Bois-Reymond.<sup>3</sup> The pendulum myograph, as its name implies, and as constructed for the author by Hawksley, of London (Fig. 308), consists of a pendulum 35 in. (90 cm.) in length, suspended by a knife edge working upon a support firmly fixed by the frame imbedded in the brick walls of the laboratory. The pendulum carries two glass (only one represented in figure) plates 15 in. (39 cm.) long, and 6 in. (15.5 cm.) wide, the outer smoked one A serving as a recording surface, the inner

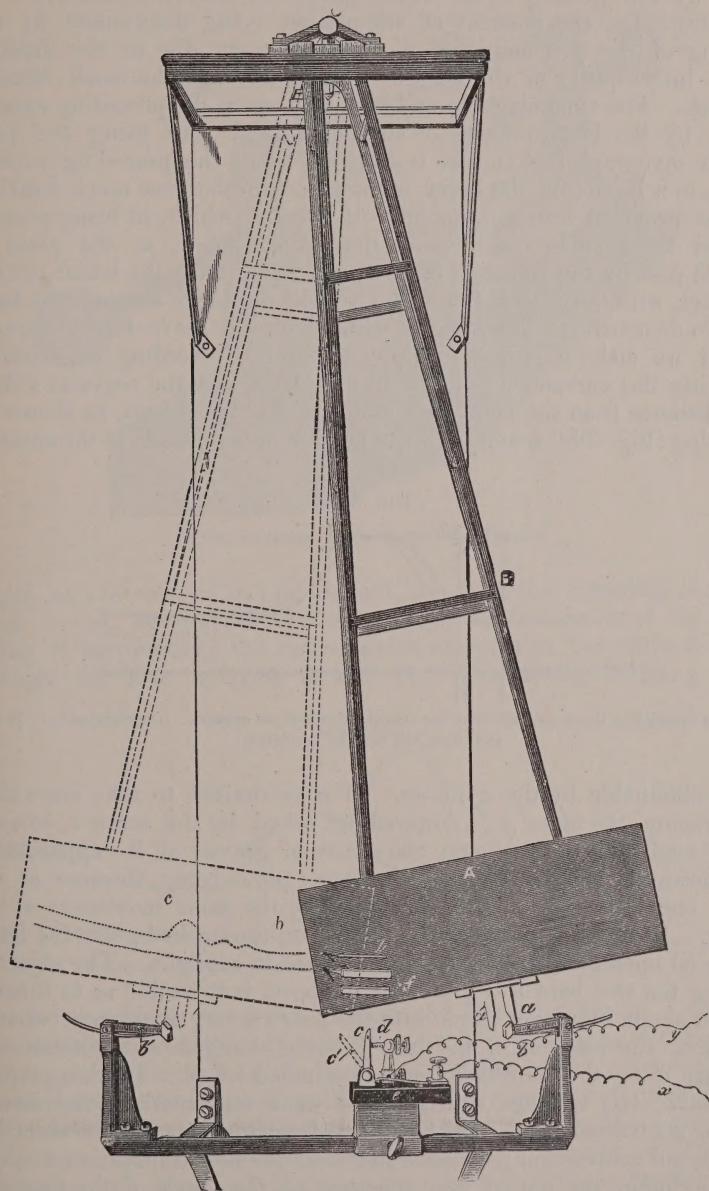
<sup>1</sup> Munk: *Archiv für Anat. and Phys.*, S. 798. Leipzig, 1864.

<sup>2</sup> *Wurzburger Verhand., Neue Folge*, ii. S. 147, 1872.

<sup>3</sup> *Op. cit.*, S. 273, Fig. 20.

one as a counterpoise. The plates, as the pendulum vibrates push to one side the two bars  $dd'$  (the latter not represented), thereby interrupting

FIG. 308.



Pendulum myograph. (FOSTER.)

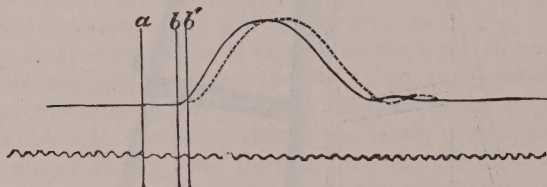
respectively the primary current of the induction apparatus, and also a current passing through the small electro-magnet, to which is attached a pen serving as a marking lever. The pendulum having



reached  $b'$  is held there by a catch similar to that which held it at  $a$  before its vibration began.

With the interruption of the primary current, the nerve is stimulated by the opening shock of the secondary current, transmitted to the electrodes, the moment of stimulation being determined by the moving of the pen acting as a marking lever, due to the simultaneous interrupting of the current passing through the small electromagnet. The time elapsing is determined, as in the preceding experiment, by the electro-magnetic chronograph  $f$ . In using the pendulum myograph the muscle is attached, as in the preceding experiment, to a lever ( $b$ ); the latter is, however, in this case much heavier, and is provided with a projecting steel point, which, in being pressed against the smoked plate makes the curved line  $c$ , as the plate is carried past by the vibration of the pendulum; after the latent period, however, with the contraction of the muscle, the nerve assumes the form  $b$ . To demonstrate the rapidity with which the nerve force is transmitted, we make use of the whippe, as in the preceding experiment, throwing the current, by means of the latter, into the nerve at a definite distance from the point first stimulated. The result, as shown by a tracing (Fig. 309) taken with the pendulum myograph, is the same as

FIG. 309.



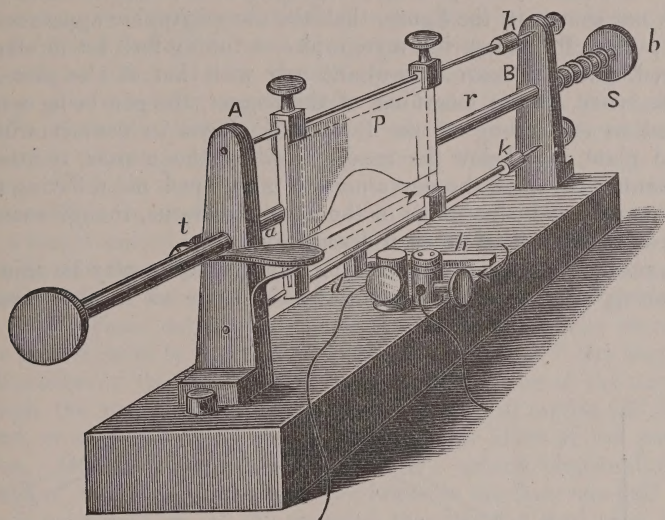
Curves illustrating the measurement of the velocity of a nervous impulse. (Diagrammatic.) To be read from left to right. (FOSTER.)

when obtainable by the cylinder. If it be desired to take more than one tracing, the plate  $g$  is lowered or raised by the screw  $s$ , so as to avoid confusing the tracings; the centre of gravity of the apparatus is not, however, thereby affected, the inner plate being elevated as the outer one is depressed, and *vice versa*, by the same movement of the screw. In order to preserve the tracing on the smoked glass, the latter is placed upon sensitive paper, and exposed to sunlight. The object of having the two bars  $d$   $d'$ , referred to above, is to enable us to throw a second single induction shock into the nerve a very short interval after the first, the position of the bar  $d'$  being changed with reference to the bar  $d$  by the movement of a graduated wheel. In this manner we obtain two tracings superimposed upon one another, the muscle having contracted twice (Fig. 309), and from which it may be seen that the second contraction took place just after the first contraction attained its maximum, the dotted line representing the course of the first contraction if the second had not occurred.

The latent period, and the velocity with which nerve force is transmitted, can also very conveniently be determined by the spring myo-

graph. In this apparatus, as constructed for the author by Plath, of Berlin (Fig. 310), a smoked glass plate ( $p$ ), 160 mm. (6.4 in.) in

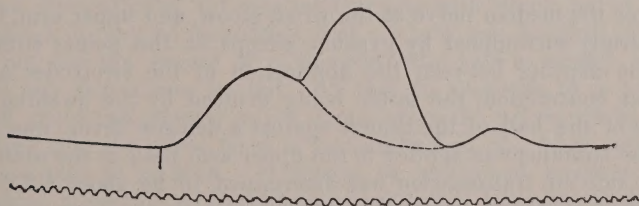
FIG. 310.



Spring myograph, as used by Du Bois-Reymond.

length, and 50 mm. (2 in.) in breadth, serves as the recording surface, being moved, however, in this instance, by the extension of the steel spring S surrounding the rod  $r$ , which moves with but little friction through the firm uprights A and B. The spring S being com-

FIG. 311.



Tracing of a double muscle curve. To be read from left to right. (FOSTER.)

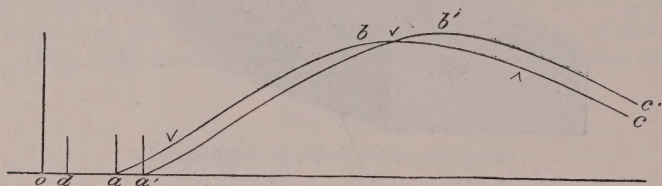
pressed by pushing it against the upright B by the button  $b$ , the rod  $r$  is thereby moved from B through A until it is caught and held by the trigger  $t$  attached to the latter. With the raising of the trigger ( $t$ ) the spring extends itself, pulling the rod  $r$  quickly through A and B, the latter carrying with it the smoked glass  $p$ . As the latter flies along from A to B, it knocks away through its projection ( $d$ ) the lever  $h$ , interrupting, therefore, the primary circuit P of the induction apparatus, and developing the secondary current S, by which the nerve is stimulated. If the glass plate be previously moved slowly from A to B until the projection  $d$  just touches the lever  $h$ , and the muscle be



made to contract the vertical trace then obtained on the smoked glass plate will indicate the moment of the stimulation of the nerve, the use of a marking lever being thereby avoided. The same method may be used in the case of the pendulum myograph. It may be mentioned, though not shown in the figure, that the chronographic apparatus used in the present form of spring myograph is a tuning-fork set in vibration by a rod, which is moved simultaneously with that of the plate, and, like the latter, by the loosening of the trigger, the pen being a needle attached to one prong of the fork, and placed in contact with the smoked plate, just below the needle to which the muscle is attached. The manner in which the nerve muscle is clamped not differing essentially from that which obtains in the other apparatus, though somewhat modified, does not need detailed description.

The results obtained by the spring myograph, as may be seen from the tracing (Fig. 312), are essentially the same as in the preceding

FIG. 312.



Tracing taken with a spring myograph.

experiments, *o d* in Fig. 312 corresponding to *a* in Fig. 309. The rate at which nerve force is transmitted has been determined by Helmholtz and Baxt,<sup>1</sup> in man as well as in the lower animals. In the case of the motor nerves this was accomplished by applying electrodes to the skin over the median nerve at the wrist, elbow, and upper arm, the arm being firmly surrounded by gypsum, except at the points stimulated. The time elapsing between the application of the electrodes and the muscular contraction, the latter being evinced by the swelling of the muscles of the ball of the thumb against a delicate lever, was greater when the stimulus was applied to the upper arm than at the wrist. The average rate of transmission was determined to be about 33.9 metres (121 feet) per second, varying, however, according to the temperature; being more rapid at a high than at a low one. The rate of transmission of the nerve force in sensory nerves was also determined by Helmholtz<sup>2</sup> in essentially a similar manner. A tactile impression being made successively upon the foot, thigh, and loins, the moment at which the sensation is felt is indicated in each instant by a movement of the finger. Now, since the time elapsing during which the impression becomes conscious perception in the brain, as well as that during which the nerve force is transmitted by the motor nerve to the finger, is the same in all three cases, the differences observed in the successive observa-

<sup>1</sup> Monatsber. d. Berliner Acad., 1867, S. 228; 1870, S. 184.

<sup>2</sup> Physio-Oecon Ges. zu Königsberg, 1850, Dec. 13.

tions must be due to the different lengths of the sensory nerves transmitting the impression, the average rate, according to Helmholtz, being about 60 metres (196 feet) per second, modified by the temperature, as in the case of motor nerves.

Knowing the rapidity with which nerve force is transmitted through the peripheral nerves, its rate of transmission through the spinal cord in man can be inferred from the difference in time elapsing during the passage of a voluntary impulse from the brain through the cord to the upper and to the lower extremity, or in the reverse direction, of an impression made upon the periphery, giving rise in the brain to a sensation. Thus, in the case of the motor fibres of the cord, if the hand be moved first in obedience to the will, and then the foot, it is evident that a longer period will elapse between the application of the stimulus, the will, and the muscular contraction, in the latter case than in the former, since, in the transmission of the nerve force through the spinal cord to the sciatic nerve, three times the distance has been traversed as in its transmission to the median nerve. In this way it has been shown by Burckhardt<sup>1</sup> that the average rate of transmission of the nerve force through the motor fibres of the cord, is about 10 metres (33 feet) per second, or about one-third of that of the motor fibres of the peripheral nerves. On the supposition that 0.08 of a second elapses during the passage of the nerve force from the brain to the foot, one-half of that time is consumed in its transmission through the cord, and one-half through the nerves. The rate of transmission through the sensory fibres of the cord does not differ very much, however, from that of the sensory fibres of the peripheral nerves. Supposing that the distance traversed through the sciatic nerve and cord from the periphery to the sensorium by a sensory impulse be the same as that of the motor impulse just referred to, the time elapsing between the application of the stimulus and the resulting sensation would be about 0.025 of a second.

As an illustration of the relative slowness with which nerve force is transmitted, it may be mentioned that a whale one hundred feet long would not feel the wound of a harpoon until half a second after the weapon was thrust into its tail, and that in response to a voluntary impulse, about two seconds would elapse before the tail would be moved, supposing that the nerve force is transmitted in the huge cetacean at the same rate as in man. It should be mentioned, however, in this connection according to Burchhardt, that tactile impressions appear to be transmitted much more rapidly through the spinal cord than painful ones, the former at the rate of 42 metres (137 feet), the latter 13 metres (42 feet) per second. The latent period and the velocity with which the nerve force is transmitted through the spinal cord being known, it becomes possible to determine approximately at least the time required for the apprehension or perception by the brain of an impression and volition. Thus, supposing the interval elapsing between the production of a sound and the hearing of the same be determined to amount to about 0.198 of a second. An apparatus being used, as represented in Fig. 313<sup>2</sup> in which the clockwork of the Hipp's chronoscope (H),

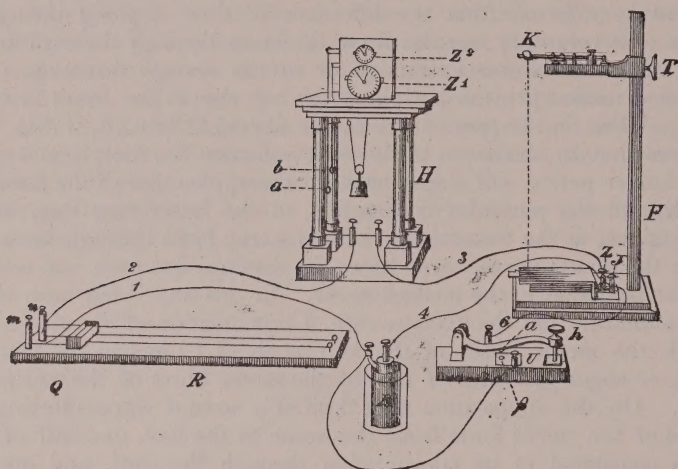
<sup>1</sup> Die Physiologische Diagnostik, S. 32. Leipzig, 1875.

<sup>2</sup> Wundt: Physiologische Psychologie. Zweiter Band, S. 231. Leipzig, 1880.



held by an electro-magnetic anchor, is set going through the weakening of the current  $K1m2H3Z4$  by the short-circuiting current  $K\beta a6JZ4$ , due to the tilting up of the board through the electrodes, by the falling of the ball, the cause of the sound, and which is stopped by the

FIG. 313.



Apparatus for determining the interval elapsing between the production and hearing of a sound.

voluntary elevation of the lever  $h$  at the instant that the sound is heard. It follows that if we deduct from the whole interval 0.198 second elapsing between the production and hearing of the sound, the time required in the mechanism of the hearing and during which the nerve force is transmitted through the cord, the motor nerves and the latent period, the remainder, or 0.112 second, will be the time required by the brain for perception and volition as follows:

|                                                       |            |
|-------------------------------------------------------|------------|
| Mechanism of hearing . . . . .                        | 0.010 sec. |
| Perception and volition . . . . .                     | 0.112 "    |
| Transmission through spinal cord . . . . .            | 0.022 "    |
| "                    "          motor nerve . . . . . | 0.044 "    |
| Latent period . . . . .                               | 0.010 "    |
|                                                       | <hr/>      |
|                                                       | 0.198 "    |

The determination of the interval between the production of a light and the seeing of the same can be determined in a similar manner by suitable apparatus.<sup>1</sup> Such determinations, apart from their physiological interest, are also of practical importance to astronomers, it being well known to the latter that considerable difference exists, amounting in some instances to as much as one second, between observations made upon the transit of a star for example, the object being seen by one observer sooner than the other. Indeed, it was such discrepancies that lead Hirsch<sup>2</sup> to determine, as far as possible, the rapidity with which

<sup>1</sup> Wundt, op. cit., S. 233.

<sup>2</sup> Bull. de la Soc. des Sciences nat. de Neufchatel, 1862.

impressions are transmitted through the optic and acoustic nerves and perceived by the brain, and of so ascertaining the personal error due to individual peculiarities, and by means of which the observation could be corrected by the personal equation, as it is called.

The determination of the rapidity with which nerve force is transmitted is a striking illustration of the advances made in physiology, due to the introduction in its study of physical methods. In the year 1844 Johannes Muller expressed the view that "we shall never have the means to determine the rapidity of nerve action, as the comparison of immense distances is wanting, by which the rapidity in the nerves can be calculated in the same respect as in the case of light,"<sup>1</sup> and yet within six years of this period what was considered impossible by one of the greatest biologists was actually accomplished, as we have seen, by Helmholtz.<sup>2</sup> It is to be observed that in the preceding experiments in which electricity was made use of as the stimulant to call into activity the nervous irritability, and muscular activity as the measure of the latter, that three distinct forces are involved, electricity, nervous and muscular force. That the electricity acts simply as a stimulant is evident, since it is only transmitted across the nerve transversely from electrode to electrode, and that the nerve force is gradually transmitted from the point where the nerve is first excited by the electricity to the muscle, is equally well shown by the length of time that is required by the nerve force to traverse the nerve to the latter, and from the death of the nerve progressing gradually from its cut end to the muscle. Further, just as electricity is a distinct force from nerve force, so is the latter to be distinguished from muscular force. Indeed, the effect of nerve force can be prevented by curara, the latter substance probably acting by destroying the nerve endings, the muscular force, however, remaining unaffected, whereas the latter force is destroyed by sulphocyanide of potassium, the nerve force being unaffected.<sup>3</sup>

It has already been mentioned that nervous action is accompanied with the development of heat. Little or nothing more has as yet, however, been positively established as to the relation existing between the two forces, and the same may be said as to the nature of the chemical changes going on.

<sup>1</sup> Physiologie, i. 4 Aufl. S. 581. Coblenz, 1844.

<sup>2</sup> Monatsber. d. Berliner Acad., 1850, S. 14.

<sup>3</sup> Bernard : Systeme Nerveux, t. i. p. 198. Paris, 1858. Vulpian : Physiologie et comparée du Systeme Nerveux, p. 136. Paris, 1866.



## CHAPTER XXXVIII.

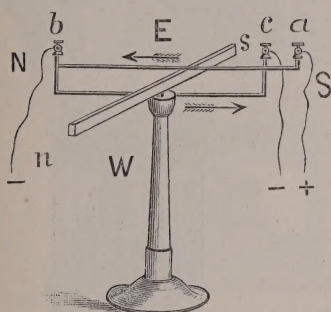
### GALVANOMETERS. NON-POLARIZABLE ELECTRODES. ELECTRICAL CURRENT. RESISTANCE. ELECTROMOTIVE FORCE OF NERVE. CAUSE OF ELECTRICAL CURRENT OF NERVE.

It will be observed, in the preceding experiments, performed with the view of demonstrating nervous irritability, that the muscular contraction following the stimulation of the nerves is the only visible positive evidence that we have obtained so far of the nerve having been modified in any way by the application of the stimulus. That some change, however, must be set up at the point of irritation and transmitted thence through the nerve, is evident from the fact of the muscle contracting in response to the stimulus, though the latter be applied to the nerve at a distance from the muscle, while from the slowness with which the irritation is transmitted through the nerve, it is to be also inferred that the change in its condition during a state of activity, whatever the nature of the change may be, is of a gradual character. If, however, the electrical condition of the nerve be examined in a state of rest, and in one of activity, it will be learned that the change induced in a nerve through its stimulation, is a change partly at least in its electrical condition, since the natural electrical current that is present in a nerve during a state of rest, disappears during one of activity. Indeed, it can be shown that as rapidly as the electrical current disappears in the nerve, the nerve current or irritability of the nerve appears, and it may be incidentally mentioned here, as confirmatory of what has just been said with reference to the disappearance of the electrical and the appearance of the nerve force, that the fact of the velocity of electricity being at the rate of 2,888,000 miles a second and of neurility of 100 to 200 feet a second, also proves the non-identity of the two. To appreciate, however, the change in the electrical condition of a nerve brought about during its state of excitement through the effect of a stimulus, it will be first necessary to explain the construction of the galvanometer, by means of which the existence of an electrical current in a cut nerve during a state of rest can not only be demonstrated, but also the amount and direction of the same determined.

The construction of a galvanometer is based upon the fundamental fact discovered by Oersted, in 1819, of a magnetic needle being deflected out of the magnetic meridian by a current of electricity passed along a wire parallel to it. Thus, for example, if an electrical current be passed above the magnetic needle from south to north as indicated by the direction of the arrows (Fig. 314, *a b*), the north pole *N* of the needle will be deflected toward the west, while if in the reverse direction, from north to south (Fig. 315, *a b*), the north pole *N* of the needle

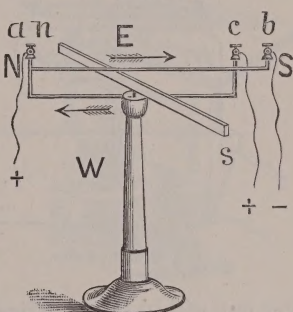
will be deflected toward the east. On the other hand, if the current be transmitted from north to south but below the needle, then the north pole of the needle will be deflected toward the west, as in Fig. 314, but if in the reverse direction toward the east, as in Fig. 315. The direction according to which the needle is deflected in either of the above cases may be easily remembered by the *memoria technica* of Ampère, according to which the north pole of the needle is always deflected toward the left of an individual supposed to be swimming in the electrical stream, and always facing the needle, the current entering the feet and leaving the head of the individual so disposed. That is to say, the north pole of the needle is always deflected toward the left of the current. It is evident, therefore, if the current be transmitted through a wire passed around the needle as arranged (Fig. 314, *a c*),

FIG. 314.



Deflection of magnet by currents.

FIG. 315.

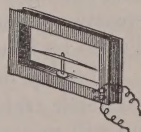


Deflection of magnet by currents.

that not only will the north pole of the needle be deflected toward the west as the current passes above the needle from south to north, but still also to the west, as the current is transmitted below the needle from north to south, and that if the wire be coiled again and again around the needle and properly insulated, the deflection of the needle will be proportionally intensified, the needle being deflected to the east if the current passes in the reverse direction, as in Fig. 315, *b c*. Hence, the name of multiplier given to such an instrument (Fig. 316), as invented in 1829, by Schweigger.

Further, since the magnetic needle is kept in the magnetic meridian by the magnetic current of the earth, the latter, in circulating around the globe from east to west, bringing parallel to itself and in the same direction the magnetic currents of the under surface of the needle, the latter finally coming to rest with the currents of its north pole opposite in direction to that of the hands of a watch, and those of its south pole in the same direction, the needle, therefore, pointing north and south, with its currents at right angles to its long axis, it is obviously of advantage in the construction of a galvanometer that if the directive influence of the earth's currents, exercised upon those of

FIG. 316.

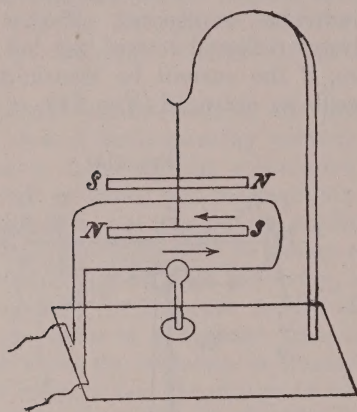


Multiplier.



the needle can be eliminated, the deflection of the needle by the directive influence of an electrical current passed through the surrounding wire will be still more intensified. This was accomplished by Nobile, in 1827, by rendering the needle, or, rather, the needles, astatic, as it is called—that is to say, two needles (Fig. 317) *NS* and *SN*, connected together, are suspended by a fine silk filament, the

FIG. 317.

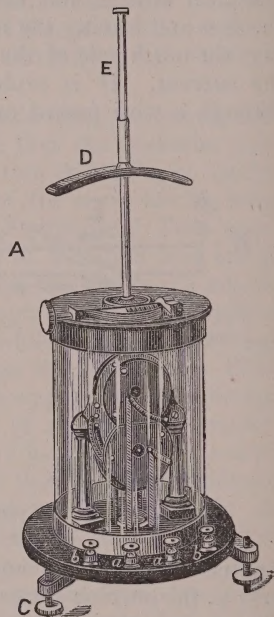


Astatic needles.

lower one within the electrical circuit, the upper one above it, so that the north pole *N* of the lower needle is opposite the south pole *S* of the upper one, and the south pole *S* of the lower needle is opposite the north pole *N* of the upper one. Such being the disposition of the needles, the influence of the earth's magnetism exerted upon the north pole of the (*N*) lower needle is more or less neutralized through the same being exerted upon the south pole (*S*) of the upper one. In sensitive galvanometers this latter effect is still more thoroughly accomplished by placing a magnet above the upper needle.

It hardly need be mentioned that, according to the Ampèrian rule, the north end *N* of the lower needle, and the south end *S* of the upper one will move together, and toward the west, if the electrified current directing them be transmitted in the direction indicated by the direction of the arrows, for, though the upper needle *SN* is subjected to the action of the two contrary currents below it, the action of the upper current being the nearest will influence it to the greatest extent. Upon the principles just enunciated are constructed the Thomson and Wiedemann galvanometers, both of which we make use of in determining the presence, intensity, and direction of the electrical currents of nerves. In Thomson's galvanometer (Fig. 318), as made for the author by Elliott, of London, the magnetic needles are very small and light, but

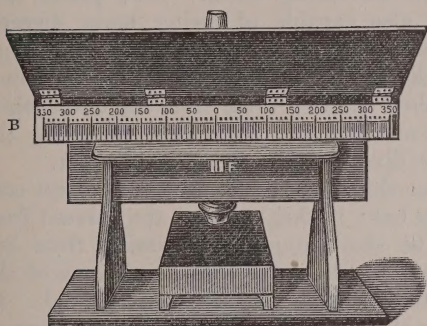
FIG. 318.



Thomson's galvanometer.

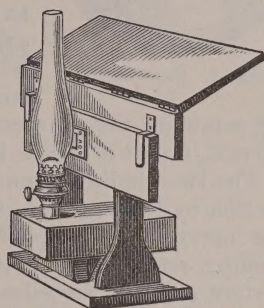
highly magnetized, and are disposed in an upper and lower set, connected by an aluminium rod, and arranged astatically. Each needle is separately surrounded by numerous coils of very fine wire, ending in the binding screws, the course of the lower coil being opposite in direction to that of the upper one. To the upper set of needles is fixed a slightly concave mirror about 6 mm., or one-fourth of an inch in diameter, serving to reflect the beam of light back to the scale B (Fig. 319), the light being transmitted from the lamp through the narrow slit F under the scale, and the lamp placed back of the scale (Fig. 320). The astatic system of needles is suspended by a single fibre of silk from a brass pin fixed to the top of the vulcanite frame of

FIG. 319.



Scale and lamp. (SANDERSON.)

FIG. 320.



Lamp and scale for Thomson's galvanometer. (LANDOIS.)

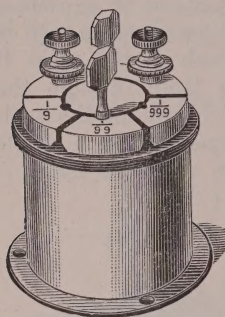
the coils. The latter are supported upon brass uprights, and are covered by a glass shade fitting into the rim of a vulcanite disk, brass bound, which is levelled by three screws (*C C*). The brass-bound glass shade covering the uprights, supports a brass rod, upon which slides a curved and weak magnet (*d*), serving to neutralize the earth's magnetism. When used, the galvanometer should be so placed that its mirror faces west, the light and scale being opposite the latter, and between two and three feet distant. The electrodes being attached to the outer two (*b b*) of the four binding screws, and the two intermediate ones being connected together, the current to be investigated will pass through the coils, the light moving from the zero along the scale to the left or right, according to the direction of the current.

If it be desired to compare the intensities of two electrical currents, then the connection between the two intermediate binding screws *a a* being unmade, the two electrodes conveying one of the currents must be attached to one of the outer binding screws, and the adjacent inner one, the other two electrodes similarly to the other outer binding screw and the adjacent inner one. If the currents be equal in intensity, and opposite in direction, the mirror will be unaffected, and the light will remain at zero, only moving to the right or left, according as one or the



other of the currents preponderates. It scarcely need be added that if a Thomson galvanometer be used in determining the presence, etc., of

FIG. 321



Shunt. (SANDERSON.)

nerve currents, the room must be darkened. Inasmuch as this galvanometer is an exceedingly insensitive instrument, it is often desirable to allow only a fractional part of the current of electricity studied to pass into it, more or less of the electricity being shunted off. In accomplishing this object we make use of the electrical shunt. This instrument (Fig. 321) consists of a series of brass plates, separated from one another, but connected by wires of different lengths, which offer, therefore, more or less resistance to a current traversing them. The plates are, however, also capable of being more directly connected by means of a brass plug. The shunt is provided with two binding screws, to which are attached the two wires from the outer bind-

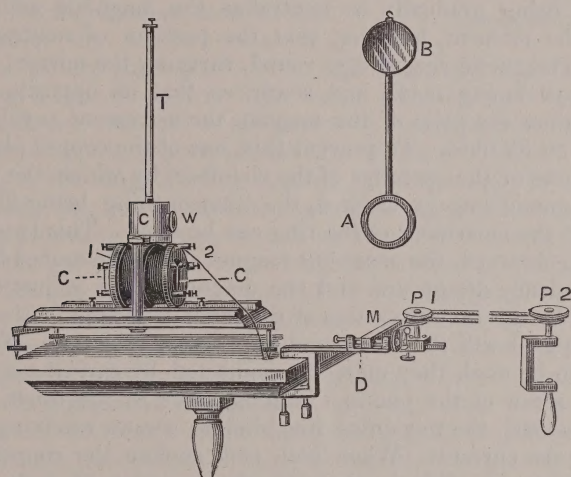
ing screws of the galvanometer and the two electrodes conveying the current, a part of which is to be diverted from the galvanometer.

The two binding screws of the shunt can be brought into direct connection by turning down a brass bar; if this be done, the current from the nerve, for example, will be short-circuited, it passing from one binding screw to the other, back to where it came from, none of the current going to the galvanometer, owing to the resistance offered. If, however, the connection between the binding screws be unmade through the raising of the bar, and the plug not placed in any of the holes of the shunt, then the current, not being able to pass directly across from one binding screw to the other, will traverse the galvanometer. The coils of the shunt being graduated, however, according to the resistance of the galvanometer, by means of the plug, we can vary at will the proportional amount of the current going to the galvanometer to that short-circuited, the amount depending upon the ratio of the resistance of the galvanometer to that of the shunt. Thus, for example, suppose the plug be inserted into the hole marked 1.9, then such resistance is offered in the short circuit that only  $\frac{1}{10}$ th of the total current goes to the galvanometer, the remaining  $\frac{9}{10}$ th being short-circuited; if in the hole marked 1.99, or 1.999, then only  $\frac{1}{100}$ th, or  $\frac{1}{1000}$ th, respectively, of the current traverses the galvanometer, the remaining,  $\frac{99}{100}$ th, or  $\frac{999}{1000}$ th, being short-circuited.

Weidemann's galvanometer, made for the author by Plath, of Berlin, consists of a thick cylinder of copper (Fig. 322), through which a tunnel is bored, the latter capable of being closed at each end by either a cover with glass front, or by a solid plug of copper. Within the copper tunnel hangs a magnetized ring (Fig. 322, A), of such size that it can just swing clear of the sides. The object in making the magnet ring-shaped is to make it stronger in proportion to its size, the centre, or inactive portion of the magnet, in that form being absent. Connected with, and passing upward from the magnetized ring through a copper tube, is an aluminium rod, terminating in a light frame holding a

circular plane mirror, facing east and west (B). In order to prevent currents of air moving the mirror, the latter is inclosed within a circular brass cover (C) having a circular window (W), through which the mirror can be viewed. Above the mirror is screwed a long glass tube (T), at the top of which there is a little windlass, supported by a small piece of ebonite, whose centring on the glass tube is effected by three screws. On the windlass a single fibre of silk is wound, passing through the ebonite and down through the glass tube, by means of which the magnet and mirror are suspended, the frame of the latter being pierced with an eye for the attachment of the platinum hook, to which the end of the silk fibre is looped. The magnetized ring can, by this means, be raised

FIG. 322.



Wiedemann's galvanometer. (McGREGOR-ROBINSON.)

or lowered or centred in the copper chamber, the latter and its attachments being supported by brass columns on a mahogany plate, levelled by three screws. The coils C, the turns of which in sensitive instruments, as in that of the author, may amount to as many as 30,000, and through which is transmitted the electricity exerting a directive influence upon the magnetized ring, are placed upon a sledge, that they can be so approximated as to meet right over the copper chamber, and when so disposed completely conceal the latter, as in Fig. 322. Since with the movement of the magnetized ring induced currents are set up in the surrounding copper chamber, opposite in direction to those of the needle, the oscillations of the latter are so diminished that after deflection it comes quickly to rest. The copper chamber is, therefore, called the damper, the close fitting of the ring within the latter and the proximity of the coils materially assisting in the dampening by it of the oscillations of the ring. Further, in order to render the magnetized ring within the copper damper astatic, we make use of the arrangement of Du Bois-



Reymond<sup>1</sup>—that is, an accessory magnet (M), a Haüy bar, is placed in the magnetic meridian horizontal to the needle, with its north pole pointing north, like that of the magnetized ring, and supported upon a bar (D) directed perpendicularly to the coils, and in a line with their axis. The accessory magnet can slide up and down the bar within its support, the bar being divided into centimetres, for measuring the extent of the movement. One end of the magnet being caught between a spring and a screw, and the latter being turned by the pulley P<sup>1</sup>, the magnet can be moved from its spring end on the other end, forming an angle with the plane of the coils, the angular movement being effected by an experimenter seated at a distance by means of the pulley P<sup>2</sup>. The galvanometer, being properly located, the accessory magnet, just described, is fixed upon its bar (B) by a clamp to the shelf. The magnet, being first placed at the end of the bar, is then slowly moved down it, the effect being gradually to neutralize the magnetic action of the earth. The moment, however, that the position of neutralization is passed the magnetic ring swings round, carrying the mirror, of course, with it, now facing north and south, so that its opposite poles are placed against the poles of the magnet, the movement involving a full half twist on its fibre. To prevent this, one of the copper plugs should be put in one of the openings of the chamber, by which the movement of the magnetic ring is blocked, the other opening being filled with a glass plug, the movement of the ring can be seen. This twisting tendency being observed, the accessory magnet should be moved back again till the tendency disappears, and the magnetic ring is just sufficiently influenced by the directive action of the earth to be kept in the meridian. The instrument will then be found to be very sensitive. When both coils are to be used, they must be connected by carrying a wire from a binding screw of the one to a binding screw of the other, according to the coils used, the remaining free binding screws receiving the wires conveying the current. When both coils enclose the copper chamber the most intense effect is obtained, the recession of coils from the chamber diminishing it.

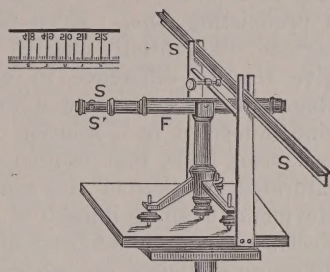
The great advantage of Wiedemann's galvanometer is that by the copper damper the disposition of the coils C, and the accessory magnet M, the magnetized ring is made aperiodic or dead beat—that is to say, the magnetic ring, when affected by the current, swings around comparatively slowly, until the maximum deflection is reached, and arriving at this point it rests there without oscillation; the current being withdrawn it swings back again to zero, stopping there without further oscillation, a current in the opposite direction being indicated should it pass the zero. It is highly important in locating the galvanometer that no iron structures whatever should be present in its neighborhood. The instrument may be placed upon a strong wooden shelf fixed to a solid dry wall, or, if the laboratory or lecture-room be upon the ground floor, upon a pillar of concrete capped with oak built upon a solid stone foundation. In using Wiedemann's galvanometer in the laboratory the extent of the deflection of the magnetized ring is observed by means of

<sup>1</sup> Abhandlungen, S. 370.

an astronomical telescope, and of a scale (Fig. 323), supported by uprights above and at right angles to the long axis of an astronomical telescope, the scale and telescope being placed upon the same table to which the pulley  $P'$ , already referred to, is attached, and which ought to be from 6 to 9 feet distant from the galvanometer. The scale being directly opposite the mirror, the reversed numbers of the former will be seen in the latter in their natural position, and with the deflection of the needle the numbers will appear as if drawn across the mirror, the amount of the deflection being indicated by the number seen in the mirror when the needle comes to rest. For lecture purposes, however, the telescope, etc., is not used, a beam from a lime or electric light being received upon a small plane mirror, is thence reflected to the mirror of the galvanometer, and from the latter to a white scale placed at a distance of from 6 to 15 feet, according to the magnification desired. In this way the deflection of the magnetic ring can be made evident to a large audience. Inasmuch as in demonstrating the presence of an electrical current in a nerve by means of the galvanometer, the current is conveyed by the wires passing from the binding screw to the nerve, it is obvious that these wires must terminate in non-polarizable electrodes—that is to say, as already has been incidentally mentioned, in electrodes that will convey an electrical current already existing in the nerve examined, but will not generate a new one when placed in contact with the latter, since the latter current so generated, extremely weak though it may be in deflecting at once the needle, the galvanometer being so sensitive, might readily be mistaken for the preëxisting current whose presence we wish to demonstrate.

In order, however, to understand the manner in which the generation of the current is prevented by the contact of the electrodes with the nerve tissue, it will be first necessary to explain what is meant by the polarization of the electrodes, to which the above effect is due. Let us suppose that two platinum electrodes have been immersed in acidulated water, and that the electricity transmitted from the battery has decomposed the water, the positive pole being covered with bubbles of oxygen, and the negative with bubbles of hydrogen. If suddenly, now, the electrodes be disconnected with the battery, and connected with a galvanometer, the direction in which the needle of the latter is deflected will indicate the presence of a current, opposite in direction to that of the battery and weakening the latter, developed through the fact of the negative pole coated with hydrogen becoming positive to the positive pole covered with oxygen, just as in the case of non-constant batteries already referred to. It is the change in the condition of the electrodes which is known as their polarization, and which occurs in a similar manner if a nerve be placed upon two copper wires. We shall see hereafter

FIG. 323.

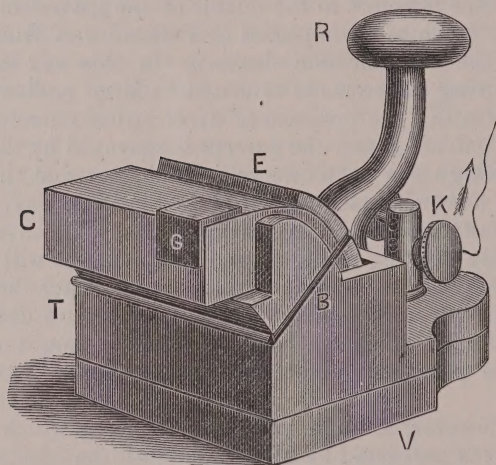


Telescope and scale.



that when a fresh muscle is connected with the galvanometer by copper wires, the deflection of the needle ensuing indicates the presence of a current, but which, on account of the polarization of the electrodes, may be as much due to the generation of a current as to the presence of a preëxisting one. Even perfectly clean platinum electrodes soon become differentially affected by contact with organic tissues, and so give rise to difference in electrical tension or electromotive force. Regnault, however, showed in 1854, that a strip of chemically pure zinc immersed in a solution of neutral zinc sulphate, and Matteucci, two years later, that ordinary zinc amalgamated and immersed in a saturated solution of the same, exhibited no polarization. Du Bois-Reymond<sup>3</sup> availing himself of these discoveries, devised non-polarizable electrodes, convenient forms of which, known as diverting vessels and diverting cylinders, are represented in Figs. 324 and 325, and by which no currents are generated when nerve or muscle is placed in contact with the same. A diverting vessel (Fig. 324), as made by Plath, of

FIG. 324.



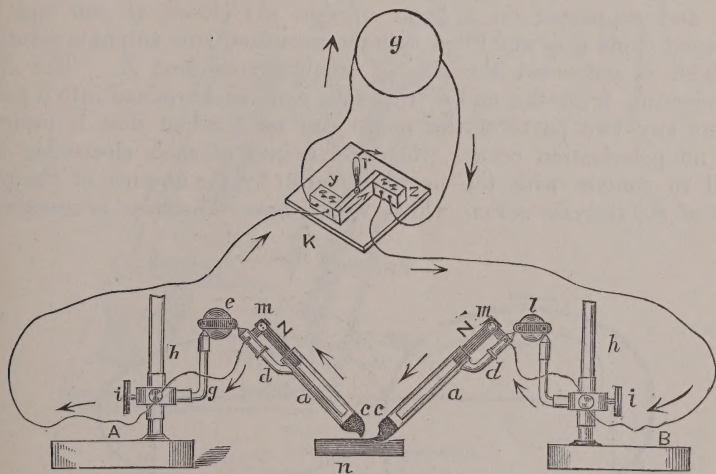
Homogeneous diverting vessel, as used by E. Du Bois-Reymond.

Berlin, consists of a zinc trough (T), containing a saturated solution of zinc sulphate, the inner surface of the trough being carefully amalgamated, and the outer surface coated with a layer of black varnish, the object of the latter being to prevent the sulphate solution coming in contact with any unamalgamated zinc.

It may be mentioned incidentally in this connection that the amalgamating fluid used is that known as Bergot's, prepared by dissolving at a gentle heat 200 grammes of metallic mercury in a 1000 gramme mixture consisting by weight of one part of nitric acid to three parts of hydrochloric acid, and adding then 1000 grammes of the latter acid. The fluid should be kept in a cool, dark place, to avoid decomposition. The trough, insulated by a base of vulcanite (V), and provided with a binding screw (K), can be lifted by a handle (R).

The insulated cushions (C), called deriving cushions, are made up of a series of layers of white Swedish filtering paper, which are stitched together at one end to secure them, and their sides cut perpendicularly with a sharp razor, and soaked in the zinc solution and squeezed so as to get rid of the bubbles of air which would offer resistance to the current. These cushions fill up the cavity of the trough, and project over the lip of the latter, a plate of ebonite (E), and an India-rubber band (B) retaining the cushion in this position. Inasmuch, however, as the nerve to be examined, if placed directly upon the deriving cushion would be corroded by the zinc sulphate solution in which the cushion has been soaked, a guard (G) is made, consisting, as already mentioned, of china clay worked up into a soft mass with  $\frac{1}{2}$  or 1 per cent. solution of common salt, which when freed of bubbles of air and flattened into a sheet (s) is folded over the cushion. A small piece of mica may also be placed upon the clay guard to limit the part to be touched by the tissue. The clay

FIG. 325.



Diverting cylinders. (E. DU BOIS-REYMOND.)

guard not only prevents the corrosion and destruction of the nerve, but through the presence of the salt, the secondary resistance, which would otherwise arise between the liquid conductor and the tissue, and diminish the intensity of the current to be examined is avoided, the salt at the same time being a good conductor. Two diverting vessels being so prepared, a fine silk-covered copper wire is carried from the binding screw (K) of one of the troughs (T) to one side of the Du Bois-Reymond key, and another wire from the other trough (T'), not represented, to the other side of the key, wires being also carried from the key K to the binding screws of the galvanometer *g*, as in Fig. 325. Such being the disposition of the diverting vessel, the key and galva-

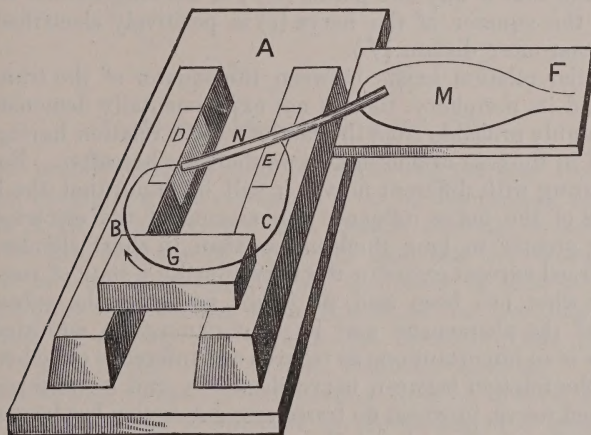




having been connected as represented in Fig. 325, and a freshly prepared nerve (*n*) having been placed upon the cushions or in contact with the points of the cylinders so that its transverse section or cut end is in contact with one of the cushions or cylinders, and its longitudinal uninjured surface at the equator with the other, with the opening of the key the needle of the galvanometer will at once be deflected, and in a direction which shows that the electrical current in the nerve passes, as indicated by the arrows (Fig. 326), from the longitudinal surface of the nerve (*a*) through the galvanometer to the transverse cut surface (*xy*), the remainder of the circuit being completed by the nerve itself (*Z*). In this connection it may be mentioned that the galvanometer is not indispensable, if we wish simply to demonstrate the electrical nerve current, as it may be accomplished by what is known as the physiological rheoscope, which is prepared in the following manner:

Upon an insulated glass plate *A* (Fig. 327) are placed two pieces of blotting paper (*B C*) soaked in salt solution, which support two albu-

FIG. 327.



Physiological rheoscope.

minous guards (*D E*), upon which rests the nerve (*N*) of a nerve muscle preparation, the cut end of which is in contact with the pad *D*, the longitudinal surface with the pad *E*, the muscle (*M*) being supported by the glass plate *F*, also insulated.

The nerve being so disposed, with the alternate connection and disconnection of the two pieces of blotting paper (*B C*) by a third piece (*G*), the muscular contraction that follows in both instances indicates the presence of an electrical current in the nerve passing in the direction of the arrows.

Returning now to the case of the nerve when in connection with the galvanometer (Fig. 326), and experimenting a little further by changing the position of one or both of the electrodes, it will soon be learned that while the current always passes from the longitudinal to the transverse



cut surface, the amount of the deflection of the galvanometer needle varies very much according to the position of the electrodes. In certain positions, indeed, as where the electrodes are placed on different sides of the nerves exactly opposite to each other ( $ab$ ), or on points equidistant from the equator ( $ef$ ,  $xy$ ), the needle is not deflected at all, there being no difference of electrical potential at such places. Such was also supposed to be the case with reference to the contents of the nerve; Recently it has been shown, however, by Du Bois-Reymond and Mendelssohn<sup>1</sup> that a current passes through the nerve from transverse section to transverse section, to which the name of "axial stream" has been given by these observers. On the other hand, if one electrode remaining at the cut surface, we move the other along the longitudinal surface toward the equator the deflection of the needle will be increased, the maximum being reached when the electrodes are at the equator of the longitudinal and transverse surfaces, as in the experiment represented in Fig. 326,  $ab$ . Experimentally, in this way, with the galvanometer, it may be learned that all parts of the longitudinal surface of any nerve are positively electrified with reference to the transverse cut surface, and that if any two points ( $ef$ ) of the longitudinal surface, that nearest the equator of the nerve ( $e$ ) is positively electrified with reference to that more distant ( $f$ ).

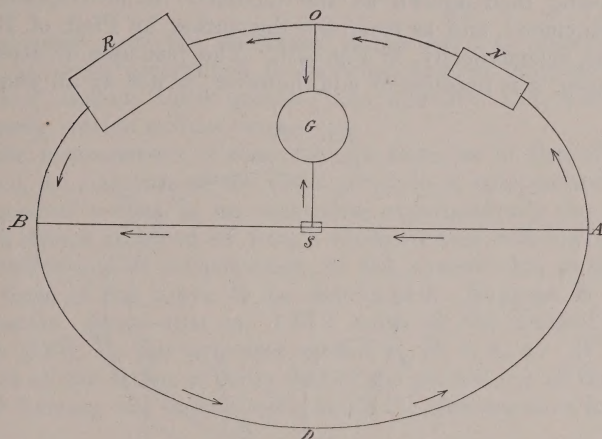
That a similar relation exists between the equator of the transverse cut surface and its periphery, though not experimentally demonstrated, is rendered highly probable from the fact of such a relation having been demonstrated in the case of muscles, as we shall see hereafter. Further, by experimenting with different nerves it will be found that the length and thickness of the nerve influence the amount of the electrical current, it being greater in long thick nerves than in short slender ones. That an electrical current exists in the nerve during a state of rest there can be, after what has been said, no doubt, whatever the subsequent explanation of the phenomena may be; but it must be admitted, and the admission is an important one as regards any inference to be hereafter drawn as to the relation between nerve electricity and nerve force, that in an uninjured nerve, in which no transverse cut section has been made, there is no evidence of an electrical current. As might be supposed, the nerve offers a resistance to the passage through it of an electrical current, and the manner in which this is determined may be considered as appropriately here as elsewhere. This is accomplished by essentially the same method as ordinarily made use of in determining the amount of resistance offered by bodies in general to the passage of electricity, and is briefly known as that by the Wheatstone's bridge. This method is based upon the principle of so disposing the body whose resistance is to be determined, that the current of electricity traversing it passes through a galvanometer in an opposite direction to that traversing a body whose resistance can be varied, until the current traversing the body exactly neutralizes the former current, as shown by the galvanometer's needle remaining at zero.

Such being the case, the unknown resistance is then equal to the

<sup>1</sup> Reichert and Du Bois-Reymond: Archiv, 1885, separat-abdruck.

known one, otherwise there would be a deflection of the magnetic needle according as the one body would offer a greater or less resistance to the current than the other. Thus, supposing that the apparatus be arranged as in Fig. 328, then the current from a Daniell's element *D*, on arriving at *A*, the end of the long wire *AB*, or rheocord, splits

FIG. 328.



Schema for determining the resistance of nerve.

into two branch currents, one of which will traverse the body *N*, a nerve for example, whose resistance is to be determined, and the other the wire *AB*. Further, the first branch current, on arriving at *O*, will divide into two, one of which will pass into the resistance box *R*, the other into the galvanometer *G*; the latter current being opposite in direction to that coming from *S*, one of the two branch currents into which the current *AS* divides, the remaining one passing from *S* to *B*, and thence back to the Daniell's element. But, as the resistance offered to the current passing from *A* toward *B* can, as we know, be increased or diminished by the sliding of *S* from or toward *A*, all the current returning to the battery when the slider is at *A*, by varying the position of the slider a point will be reached on the wire, as at *S*, when the galvanometer needle will remain at zero, showing that the current passing down from the nerve from *O* to the galvanometer is equal and opposite in direction to that passing up from the wire at *S*. Such being the case, then the resistance offered by the nerve, or *x*, is to that of the resistance offered by the wire *AS* is to the part *SB*—that is,  $x : R :: AS : SB$ . Now, as the resistance *R* is learned by observing the number of plugs out, and that of *AS* and *SB* being also known, the rheocord wire having been previously graduated, the unknown resistance of the nerve, or *x*, is given in terms of *R*, *AS*, and *SB*, as shown by the equation

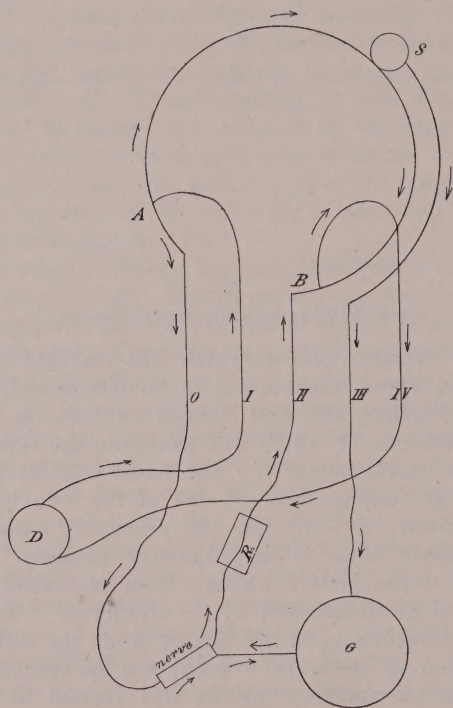
$$x = \frac{R \times AS}{SB}.$$

<sup>1</sup> Or if *AS* and *SB* be constant and equal, then the resistance of *N* equals that of *R*, and can be inferred from that of the latter as determined by the number of plugs out, as in the form of resistance box made for the author by Hartmann, of Marburg.



The method just described of determining the resistance offered by a nerve, for example, to the passage of a current of electricity is at times inconvenient, even quite awkward, on account of the length of the rheocord wire involved. This is readily obviated, however, as suggested by Du Bois-Reymond, by disposing the wire in the form of an arc, the latter, with the accessory binding screw *O*, Christiani's modification, being then known as the modified round compensator of Du Bois-Reymond, and as made for the author by Pfeil, of Berlin, is represented, schematically, in Fig 329. The principle of determining the resistance, it is needless to add, however, is not at all affected by

FIG. 329.



$$Ne : R :: AS : SB$$

Schema of round compensator, with Christiani's modification.

this modification of Du Bois-Reymond and Christiani, the difference between the long and round rheocord or compensator being simply in the disposition of detail. Thus, if Fig. 329, a schematic representation of the round compensator, be compared with Fig. 328, the long one, it will be observed that in both instruments the current from the Daniell's element *D*, on arriving at *A* splits into two currents, one of which passes to the wheel or slider *S*, the other to the nerve; that the current at *S* divides into two, one of which passes to the galvanometer *G*, the other back to the Daniell's element; that the current after traversing the nerve divides into two, one of which passes to the gal-

vanometer  $G$ , the other to the resistance box  $R$ , and thence back to the Daniell's element; that the two currents, passing in opposite directions through the galvanometer neutralize each other. It follows, therefore, that in using the modified round compensator we obtain the same proportion as in using the long one, viz.:

$$x : R :: AS : SB, \text{ or } x = \frac{R \times AS}{SB}.$$

The value of  $x$ , or the resistance of the nerve, as obtained by this method, has been ascertained to be, when exerted longitudinally, two and a half million times greater than mercury, and, when exerted transversely, twelve million times.

For the measurement of electromotive force, as in that of electrical resistance, we make use of the same principle of compensation, or that of Poggendorf<sup>1</sup>—that is, we determine experimentally the amount of a branch stream switched off from a rheocord wire sufficing exactly for the neutralization, or compensation, of the current due to the electromotive force of the nerve to be determined. Suppose  $E$  to be the electromotive force—that is, 1.079 volts of the Daniell's element  $D$  (Fig. 330), in the principal circuit  $a, D, b, c, a$ ;  $W + w$ , the resistance of the latter,  $w$  being that of the portion  $ac$  of the rheocord wire  $ab$  forming the short circuit, and  $e$  the electromotive force of the

FIG. 330.

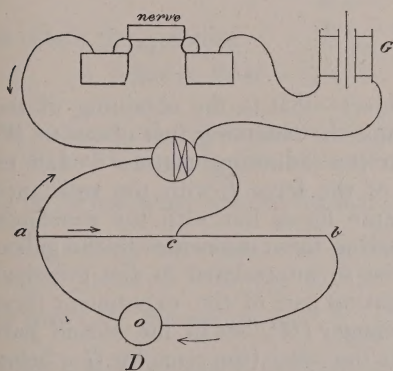
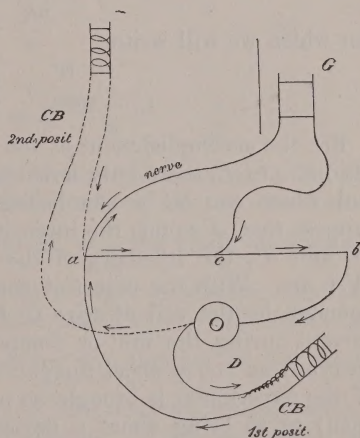


FIG. 331.



Diagrams to illustrate the determination of electromotive force.

nerve  $n$  to be compensated, then, according to Kirchoff's theorem of branched currents, as the conditions of compensation, we obtain the equation

$$e : w :: E : W + w,$$

and as  $e(W + w) = wE$

$$e = \frac{w}{W + w} \times E. \quad (1)$$

<sup>1</sup> Du Bois-Reymond: Gesammelte Abhandlungen, Erster Band, S. 176, S. 257.



If now  $W+w$  be constant—that is, if the rheocord wire, with its now short-circuiting part belongs to the principal circuit—then

$$e = \frac{w}{G} \times E$$

that is to say, the electromotive force  $e$  of the nerve to be determined is directly proportional to the resistance  $a c$  of the short circuit. In order, however, to measure this force  $e$ —that is, to determine the ratio of  $e$  to  $E$ , as the ratio of  $w$  to  $W+w$  is not directly obtainable, we proceed in the following manner:<sup>1</sup>  $E$  being the electromotive of the Daniell's element  $D$  (Fig. 331),  $e$  the electromotive force of the nerve to be determined,  $G$  the galvanometer,  $a b$  the rheocord wire, and  $c$  the slider, let us determine the position of the latter when  $e$  is compensated—that is, when no current passes through  $G$ . Suppose, now, that compensation be effected when the slider is at  $c$ , and that  $W$  be the resistance of the conductor  $a C B$ ,  $D b$  (Fig. 331, first position),  $N$  the length of the wire  $a b$  in millimetres,  $n$  the length of the part  $a c$ , and  $w$  the resistance of a millimetre of wire, we will then obtain from equation 1 the equation 2:

$$e = \frac{n \times w}{W + Nw} \times E \quad (2)$$

or since

$$e (W + Nw) = nwE$$

$$\frac{W + Nw}{nw} = \frac{E}{e} \quad (3)$$

but which we will write

$$\frac{W}{nw} + \frac{N}{n} = \frac{E}{e}. \quad (4)$$

For the accomplishment of our object—that is, the obtaining of the ratio of  $e$  to  $E$ , there only now remains the obtaining that of  $nw$  to  $W$ , and which can be accomplished in the following manner: Let us suppose that  $J$  equals the intensity of the force  $E$  with the resistance  $W$  and  $J'$ , the intensity of the same force, but with the resistance  $W+nw$ . With the object of comparing these intensities by the galvanometer, let the coil of wire  $C B$  be so intercalated in the principal current during the first or compensating part of the experiment (first position) as not to affect the galvanometer ( $G$ ), but in the second part of the experiment is brought so near the latter (the circuit  $a G c$  being open) as to bring about a deviation of the magnetic needle (second position). The coil  $C B$  being so shifted from the first to the second position, we obtain the intensity  $J'$ , corresponding to the resistance  $W+nw$ , while the coil  $C B$  remaining in the second position, if the wire  $ab$  be taken out of the circuit, then we will obtain the intensity  $J$ , corresponding to the resistance  $W$ , and since the intensities are inversely as the resistance, we get the equation:

$$\frac{J}{J'} = \frac{W + Nw}{W} \quad (5)$$

<sup>1</sup> Du Bois-Reymond, op. cit., S. 176.

<sup>2</sup> Hermann: Handbuch, Erster Band, Erster Theil, S. 188. Leipzig, 1879.

but which we will write in the form of

$$\frac{J}{J'} = \frac{1 + Nw}{W} = 1 + \frac{N}{n} \times \frac{nW}{W} \quad (6)$$

or calling the ratio

$$\frac{J}{J'} = M$$

$$M = 1 + \frac{N \times nw}{nW} \quad (7)$$

or since

$$(M - 1) n W = Nnw$$

$$(M - 1) \frac{n}{N} \times W = nw \quad (8)$$

Substituting this value of  $nw = (M - 1) \frac{Wn}{N}$  in equation (4)  $\frac{E}{e} = \frac{W}{nw} + \frac{N}{n}$  we obtain

$$\begin{aligned} \frac{E}{e} &= \frac{W}{(M - 1) \frac{Wn}{N}} + \frac{N}{n} = \frac{WN}{(M - 1) Wn} + \frac{N}{n} \\ &= \frac{WNn + (M - 1) \frac{WnN}{n}}{(M - 1) Wn \times n} = \frac{WNn + M Wn N - Wn N}{n (M Wn - Wn)} \\ &= \frac{M W N}{M Wn - Wn} = \frac{M W N}{(M - 1) Wn} = \frac{M}{M - 1} \times \frac{N}{n} \end{aligned}$$

and which last value enables us to determine the electromotive force of the nerve, since from

$$\frac{E}{e} = \frac{M}{M - 1} \times \frac{N}{n} \quad (8)$$

we obtain the equation

$$eMN = E(M - 1)n \quad \text{or} \quad e = E \frac{(M - 1)}{M} \frac{n}{N} \quad (9)$$

that is to say, the electromotive force of the nerve ( $e$ ) is equal to that of the Daniell's element ( $E$ ), multiplied by the ratio of the two intensities

$\frac{J}{J'}$  or  $M$  less unity divided by that ratio  $M$ , and the result multiplied

by the ratio of the number of millimetres of the compensator portion of the rheocord wire ( $n$ ) to the whole number of millimetres in

the wire ( $N$ ), the expression  $\frac{M - 1}{MN}$  giving the fraction of the force

of the Daniell's element each millimetre of the rheocord wire is worth, and is called, therefore, the graduation constant.<sup>1</sup> It suffices to measure once in the manner described a constantly easily reproducible force ( $e$ ), for example, that of a thermopile, of a difference of 100, and by means of this force to learn the graduation constant of the apparatus by determining the length of the rheocord wire—that is,  $n$  or the number of millimetres necessary for compensation. Suppose, for example, that we have determined ( $e$ ) to be equal to the  $\frac{1}{15}$  of a Daniell, and 560 millimetres equal  $n$  to be necessary for compensation, then each millimetre equals the  $\frac{1}{15}$  of  $\frac{1}{560}$  or  $\frac{1}{8400}$  of D. Finally, by means of a

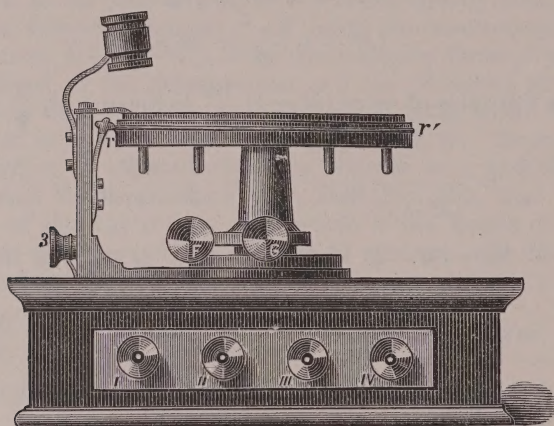
<sup>1</sup> Du Bois-Reymond, op. cit., S. 261; Idem, Zweiter Band, S. 235.



resistance box introduced into the circuit, the fraction  $\frac{1}{8400}$  can be made a more convenient one,  $\frac{1}{10000}$  for example, by which the calculation will be facilitated.

In endeavoring to explain the manner in which the electro-motive force of a nerve is determined and the rheocord wire graduated, we have supposed, for the sake of simplicity, that the rheocord used is the long straight one, such as represented in Figs. 330 and 331. As in the case of

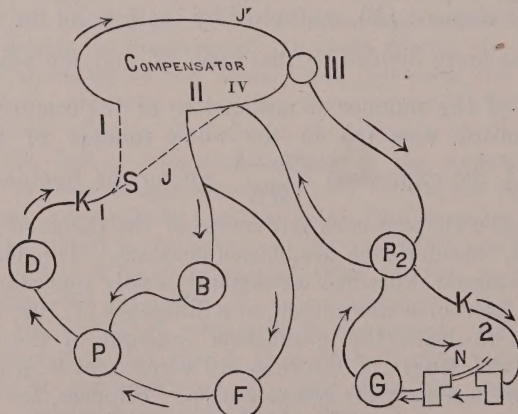
FIG. 332.



Du Bois-Reymond's round compensator.

the measurement of electrical resistance, so in that of the electromotive force, it will be found, however, that the round compensator of Du Bois-Reymond is a much more convenient instrument. When used,

FIG. 333.



Scheme for determining electromotive force of round compensator.

however, for the latter purpose the attachment O (Fig. 329) is left out of the circuit. That is, the instrument is used in its original form

(Figs. 332, 333), without Christiani's modification. As an illustration of the manner of using the compensator in this form let us suppose :

$E$  = the electromotive force of a Daniell's element.

$e$  = the unknown electromotive force.

$W$  = the resistance of the circuit without the short-circuiting wire of the compensator.

$J$  = the intensity of the current excluding the short-circuiting wire of the compensator.

$J'$  = the intensity including the latter.

$n$  = the number of divisions on the graduated scale necessary for compensation.

$N$  = 1000 the length of the short-circuit wire of compensator.

Then by substituting in equation (9), p. 589, for  $M$  its value  $\frac{J}{J'}$  we shall obtain the equation (10)

$$e = \frac{n}{N} \times \frac{J - J'}{J} \times E \quad (10)$$

Since

$$\frac{J - 1}{\frac{J}{J'}} = \frac{J - J'}{\frac{J'}{J}} = \frac{JJ' - J'^2}{JJ'} = \frac{J - J'}{J}$$

from which equation  $e$  can be obtained after  $n$ ,  $J$  and  $J'$  have been determined experimentally. With the view of accomplishing this object the compensator, etc., are disposed as in Fig. 333.<sup>1</sup> We will suppose that the current from the Daniell's element D enters the compensator at I, and after traversing the wire on arriving at III divides into two currents, one of which (III IV II F P) returns directly to the battery, the other (III P<sup>2</sup> K<sup>2</sup> N G P<sup>2</sup> IV II) indirectly, first passing through the galvanometer in the opposite direction to that of the nerve current, and exactly neutralizing the latter, the needle being brought to zero, the wheel of the compensator being at III. Such being the case, it is only necessary in order to obtain the value  $n$  to read off the divisions of the scale between zero and III. It remains now to obtain the values of  $J$  and  $J'$ . To do this we open K<sup>2</sup> and turn down the whippe P in such a way that B is included in the circuit, F, however, being left out. That being done according further as the Daniell's element is connected with IV or I, by the shifting of the brass piece S, the current will pass respectively through D S IV II B P D, with the intensity  $J$ , or through D S I III IV II B P D, with the intensity  $J'$ . It may be mentioned incidentally here that the coil B having the same resistance as that of F, consists of only two coils, but of thick wire, and that it should be placed at such a distance from the magnet, and at such an angle to the plane of the magnetic meridian, that the deviations of the needle will not exceed 300 seconds. The electromotive force of the sciatic nerve of the frog as determined by the compensator amounts, according to Du Bois-Reymond,<sup>2</sup> to 0.022 of a Daniell cell, that of the rabbit not exceeding 0.026 D. According to the recent elaborate researches of

<sup>1</sup> Du Bois-Reymond, op. cit., S. 257.

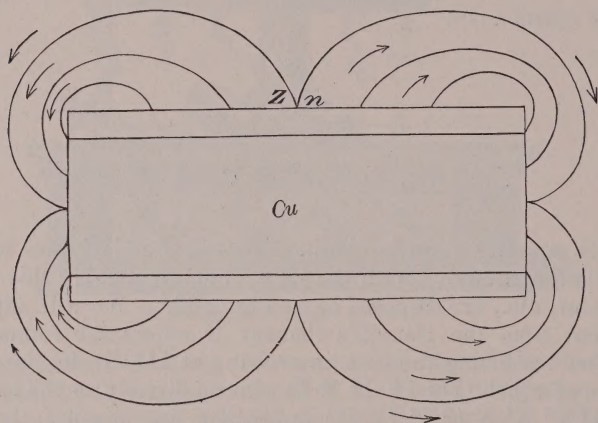
<sup>2</sup> Idem, Zweiter Band, S. 232.



Mendelsohn,<sup>1</sup> made at the suggestion of Du Bois-Reymond, the electromotive force of the axial current of the posterior roots of the spinal nerves of frogs—that is, of the current from equator to central or peripheral transverse section amounts respectively to 0.00893, and 0.00767 of a Raoul, that element (copper in copper sulphate solution, and zinc in zinc sulphate) being used instead of a Daniell.

Having considered the electromotive force of the nerve, the nerve current, and the resistance offered by the nerve to the passage of electricity, it remains for us now to offer, if possible, some explanation of the natural nerve current based upon its physical structure. It is well known that if a solid copper cylinder (*Cu*, Fig. 334), covered except at its ends by a layer

FIG. 334.



of zinc *Zn*, be immersed in a conducting fluid like water, that electrical currents are developed, which, as may be shown by the galvanometer, pass from the longitudinal or zinc surface to the transverse copper one, and that, according as the electrodes are shifted from point to point of its copper and zinc surfaces these currents become stronger, weaker, or disappear altogether, and that while if the copper be entirely covered by its zinc mantel there is no appreciable electrical current, however the electrodes may be placed. In a word, the physical apparatus just described, as regards its electrical conditions exactly resembles a nerve. When it is remembered that the ultimate nerve fibre consists histologically of the axis-cylinder surrounded by the white substance of Schwann and neurilemma, it might appear at first sight that one or the other of these two membranes bears to each other, or to the axis-cylinder, the same relation electrically that we have seen the outer zinc mantel does to the copper axis of the simple physical apparatus just described.

That such, however, is not the case, is proved by the fact that even at the nodes of Ranvier in the spinal nerves, and in the sympathetic fibres also, where the white substance of Schwann is absent, neverthe-

<sup>1</sup> Ueber den axialen Nervenstrom, Maurice Mendelsohn, 1885, Archiv f. Anat. und Phys.

less, electrical currents can be shown to exist, evidently then it cannot be the contact of the substance of Schwann with either the neurilemma or the axis-cylinder that is the cause of the difference in the electrical potential, while the presence of electrical currents in the cord in the absence of the neurilemma equally shows that the contact of that membrane with the axis-cylinder has nothing to do, any more than the white substance of Schwann, with the development of such currents. The only conclusion to be drawn from such facts is that of the three parts of which the nerve consists, it is the axis-cylinder only which is concerned in the development of the electrical current, and which confirms the conclusion that we have come to upon other grounds that it is functionally the most essential part of the ultimate nerve fibre, and that the electrical current developed in a nerve in which a transverse section has been made, is due to the fact of the negatively electrified axis-cylinder being then exposed to the positively electrified nutritive fluid surrounding it, since, as we have just seen, the difference between the longitudinal and cut surfaces electrically cannot be attributed to the contact of either neurilemma or substance of Schwann with the axis-cylinder. If such be the case, it becomes intelligible why, as we have already mentioned, there is no appreciable electrical current in the uninjured nerve—that is, in one without a transverse cut section, since under such circumstances the negative axis-cylinder is not exposed to the positive nutritive fluid surrounding the nerve, just as in the case of the physical apparatus (Fig. 334). There is no electrical current developed as long as the negative copper axis or core is completely enveloped by the positive zinc mantel or hull. As an illustration of the influence of the contact of a surrounding fluid upon a tissue in the development of an electrical current, it may be here mentioned that if the transverse cut surface of a dried muscle be placed upon the surface of distilled water, that an electrical current will be developed, passing from the longitudinal to the cut surface as soon as the muscle begins to swell through imbibition of the fluid with which its transverse section is in contact. While the explanation just offered, that of Gruenhagen,<sup>1</sup> is considered by that physiologist as satisfactorily explaining the electrical condition of the cut nerve, however plausible it may appear, it must be mentioned that it is not accepted by all physiologists. Thus, Du Bois-Reymond,<sup>2</sup> the highest living authority on electro-nerve physiology, has for many years held that the nerve consists not of a homogeneous axis, surrounded by a hull like that of the physical apparatus just described (Fig. 334), but of a series of electro-motive double dipolar molecules, imbedded in an indifferent and imperfectly conducted medium. Each double molecule consists of a positive and negative part, being so disposed, as may be seen from (Fig. 335), that the two positive parts of the two halves are placed together within, the two negative parts without, as it were, the double molecule presenting then a negative surface at the transverse section or cut end, and a positive surface at the longitudinal surface or section of

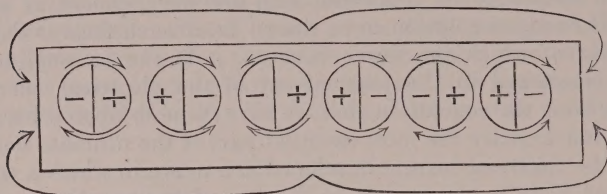
<sup>1</sup> Funke: Physiologie, Erster Band, 1876, S. 487.

<sup>2</sup> Untersuchungen über Thierische Electricität, Zweiter Band, S. 323. Berlin, 1849.



the nerve. Regarding the double molecule as a minute battery whose positive and negative poles are at the longitudinal and transverse surfaces, respectively, currents will be developed which through the imperfect conductivity of the medium will circulate in more or less eccentric

FIG. 335.



Electromotor double dipolar molecules.

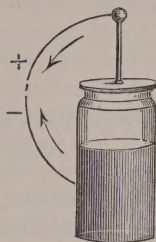
lines not only in the immediate neighborhood of each molecule, but at some distance from the latter, from the positive middle surface to the negative ends of the nerve as indicated by the arrows, and giving rise to the deflection of the galvanometer needle, as we have seen is the case when the electrodes are applied to the nerve. Suppose that the nerve does consist according to this hypothesis of molecules, such as just described, it is evident that the electrical current within it is a closed one, the nerve differing in this respect from the zinc-copper apparatus as regards any current diverted into the galvanometer. In either case the current can only be a partial one, the deflection of the needle indicating the presence of a current, but in no wise the total strength of the current due to the electromotive force of all the molecules.

That the strength of the latter must be much greater than the partial current deflecting the needle is shown by the necessity of using such sensitive galvanometers, and is implied in the overcoming of the resistance both of the nerve and the galvanometer circuit, which is considerable. Indeed, were not the total electric strength of the molecules much greater than that of the partial current, the latter would not be appreciated by the galvanometer at all. It is for such reasons that Du Bois-Reymond holds that the electromotive force of the nerve molecules exceeds that producing all other known currents, and is capable, in the highest degree, of producing all the known effects of currents. While there is much to be said in favor of Du Bois-Reymond's view of the nerve consisting of electromotive molecules, it must be admitted that it is difficult to explain on such a theory the weak currents that are developed by placing the electrodes upon different points of the longitudinal surface, and why currents of any kind are only present in the injured nerve, or one presenting a transverse section. Indeed, this latter fact, equally an objection to the view offered by Gruenhagen, has led some physiologists, like Hermann,<sup>1</sup> to deny altogether the pre-

<sup>1</sup> Handbuch, Zweiter Band, Erster Theil, S. 169. Leipzig, 1879.

existence of any electrical current in the nerve, attributing the latter to the death of the transverse cut surface, which, at that moment, becomes negative to the longitudinal surface. On the other hand, according to Radcliffe,<sup>1</sup> the electrical character of the nerve current is rather static in its nature than voltaic, the nerve being compared on this view to a charged Leyden jar (Fig. 336), the current being simply accidental, and due to the applying of the electrodes of the galvanometer to points having different electrical tensions. After all, however, the difference between static and voltaic or current electricity is not a profound one, being rather one of degree than of kind, since the former is one of high tension, but small in quantity, the latter of low tension, but large in quantity; by tension being meant the tendency of the electricity accumulated at the extremities of the electrodes to free itself.

FIG. 336.



Leyden jar.

<sup>1</sup> Dynamics of Nerve and Muscle, p. 24. London, 1871.

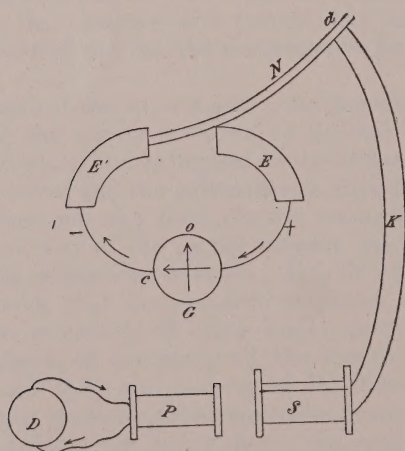


## CHAPTER XXXIX.

### NEGATIVE VARIATION. RAPIDITY OF ITS PROGRESSION. ELECTROTONIC CURRENTS. ELECTROTONUS.

HOWEVER prevailing views may differ as to the nature and cause of the electrical current present in a cut nerve during a state of rest, there is no difference of opinion as to the importance of the fact already alluded to, of the diminution or disappearance of the electrical current of the nerve during its momentary period of activity, or, as it is usually called, of the negative variation or current of action, according as the diminution in the deflection of the needle is regarded as being due to the diminution of a preëxisting natural current, or of a current of rest, developed through the nervous tissue when injured becoming negative toward that part of it uninjured. Whether the electrical current present in a cut nerve during a state of rest be a natural or an artificial one, preëxisting or developed by injury, the fact remains the same, that during the activity of the nerve its electrical current undergoes a negative variation. That the latter phenomenon is not simply an accidental

FIG. 337.

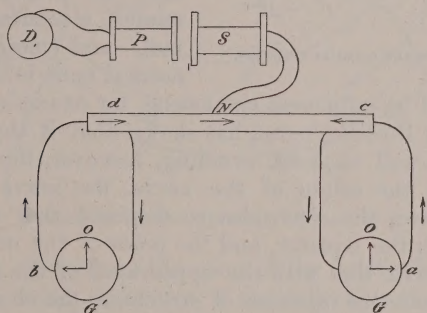


Negative variation.

one, but constitutes an essential feature of nervous action, is still further shown from the intensity of the one varying with the other, and, as already mentioned, from the rate at which the negative variation travels along the nerve being the same as that at which the nerve force itself is propagated. While the negative variation can be shown by stimulating the nerve with a single induction shock the phenomenon becomes

much more evident when the induction apparatus is used with the automatic interrupter, since the shocks thrown into the nerve succeed each other then so rapidly that before the galvanometer needle can return to its first position, that due to the electric nerve current from which it was deflected by the negative variation, it is again deflected by the latter, and consequently remains there in one position, that due to the negative variation. Thus, for example, suppose that the transverse section of the nerve  $N$  be in contact with one of the diverting electrodes  $E'$  (Fig. 337), and the longitudinal surface with the other, and that the deflection of the magnetic needle at  $G$ , due to the electrical current of the nerve during a state of rest is perfectly evident, amounting to, say  $c$ . Such being the case, if now the nerve  $N$  be stimulated by the induction apparatus  $PS$  (at such a distance ( $d$ ) as not to permit of the escape of the current into the electrodes of the galvanometer) the deflection of the needle in the reverse direction back toward zero  $O$  at once indicates that the electrical current of the nerve has been diminished, has undergone a negative variation. If now the experiment be so modified (Fig. 338) that, while the nerve is stimulated in the middle  $N$ , its two ends ( $c$   $d$ ) are in contact with the electrodes of two galvanometers

FIG. 338.



Negative variation.

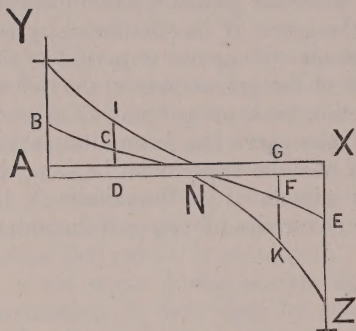
( $G$   $G'$ ), it will be observed that there is a diminution in the electrical current ( $a-o$ ,  $b-o$ ) of the nerve at both ends, showing that the disturbance in the electrical condition of the nerve, whatever its nature may be, is propagated in both directions, from the centre or the point of the application of the stimulus: a very important fact, since, if the phenomenon of the negative variation is intimately associated with that of the development and propagation of nerve force, it proves that the latter is transmitted from the point of stimulus, both to the central and peripheral ends of the nerve, confirming the view already advanced, that the nerve force is transmitted in both directions, which could not be learned obviously from the muscular contraction, and that the function of a nerve depends, not upon its intrinsic structure, but whether it terminates in a motor, sensory, or glandular organ.

By extending our experiments it will be further found that all kinds



of nerves exhibit the phenomena of negative variation, and that from every part of a nerve, during a period of rest, an electrical current can be diverted, and that it is indifferent whether the central or the peripheral end of the nerve be the excited or the diverting portion. Finally, that the amount of the negative variation  $YB, IC$ , at the different points of the nerve  $N$  will be always proportional to the amount of the preëxisting nerve current  $YA, ID$ , of which it is nothing but the diminution (Fig. 339), hence if the former current be absent there will be naturally,

FIG. 339



Curves of nerve current and negative variation.

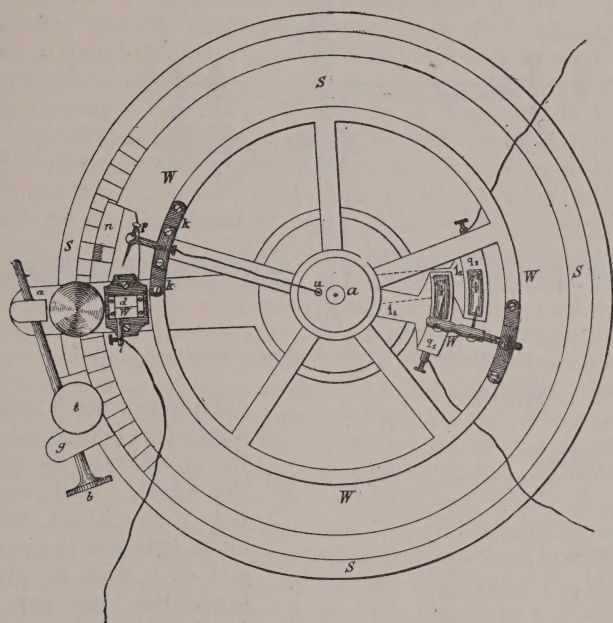
therefore, no negative variation. Such is the case, for example, if the diverting electrodes be placed upon two points of the longitudinal surface symmetrically disposed with reference to the equator, the magnetic needle not being then deflected by the nerve current, there can be no diminution of the latter or negative variation. An interesting fact as regards the phenomenon of negative variation is, that it can not only be produced by artificial stimuli, electrical, chemical, thermal, and mechanical, but by natural ones inherent in the nervous system itself by influences emanating, for example, from the spinal cord.

Thus, Du Bois-Reymond has shown that if the sciatic nerve of a living frog be well exposed, avoiding, however, the injuring of the bloodvessels and the origin of the nerve, the nerve cut through at the popliteal space, the electrodes so disposed that the point of one is in contact with the equator, and the point of the other with the cut surface of the nerve, that with the appearance of the muscular cramps due to the subcutaneous injection of strychnia, the electrical current of the nerve will undergo a negative variation. The significance of this experiment will be better appreciated, however, when the subject of reflex action has been considered; since the muscular contraction, with the accompanying variation in strychnia poisoning is due to an impression made upon the skin and thence transmitted to the spinal cord, and from that nervous centre reflected to the muscles. Further, according to the same high authority negative variation occurs during the tetanus brought about by the mechanical crushing of a nerve, or the destruction of the same by heat and during tetanus of the sciatic nerve, more especially when induced by the stimulation of its cutaneous branches. It has already been mentioned that the rapidity at which the negative variation is transmitted is the same as that of the nerve force itself. This was first determined by Bernstein<sup>1</sup> by means of his differential rheotome. The principle of this instrument consists in closing the circuit stimulating the nerve as well as that diverting its natural current, by a wheel

<sup>1</sup> Untersuchungen über den Erregungsvorgang im Nerven- und Muskel systeme. Heidelberg, 1871.

rotating at a known rate and of so disposing the two pairs of electrodes that the stimulating circuit is closed before the diverting one. The interval of time between the two being determined from the rate at which the wheel is rotating, and the negative variation being trans-

FIG. 340.



Bernstein's differential rheotome. Horizontal view.

mitted along the nerve from the point of the application of the stimulus to that of the diverting electrodes, if the deflection of the needle in the reverse direction appears at the moment that the diverting circuit is closed, the rate at which the negative variation has been transmitted from the point of stimulation to that of the diverting electrodes becomes at once known; and experimentally it was so found by Bernstein to be the same as that of the rate of the nerve force itself, viz., in the frog twenty-eight metres a second.

The differential rheotome, somewhat more in detail, as made for the author by Zimmerman, of Heidelberg, consists of a wheel (Fig. 340, *W*) having a diameter of 12.5 cm. (5 inches) horizontally disposed, whose hub or axis (*a*) is elongated vertically upward and downward, the lower end (Fig. 341, *e*) working in a mercury cup (*m*), the upper end (*r*) in the frame, the axis passing through a grooved disk (*d*), serving for the attachment of the cord of the electro-magnetic rotation apparatus to be described presently, by means of which the axis and the wheel are uniformly rotated. To the periphery of the wheel (Fig. 340) is attached a brass piece (*k*), insulated by ebonite, which carries the steel pointer (*p*), the latter being elevated or depressed by the screw and





rapidly that they may be regarded as one momentary stimulus. The periphery of the wheel *W* (Fig. 340), opposite to the brass box and wire just described, carries also an insulated bar, through which pass two sharp-pointed steel pointers ( $p^1 p^2$ , Figs. 340, 341) obliquely disposed, capable of being elevated and depressed by screws, which, as the wheel rotates, glide smoothly over the surface of the mercury in the two steel insulated cups  $c^1 c^2$ , supported by the brass arms ( $q^1 q^2$ ). In order to insure perfect contact with the mercury, the latter should be pure and renewed daily, the steel pointers should be also dipped every day in copper sulphate solution. As the steel pointers glide over the mercury, the current diverted from the nerve is then closed, the current passing (Fig. 342) from the non-polarizable electrode on the longitudinal surface (*b*), the two binding screws, through the mercury cups ( $c^1 c^2$ ) to the galvanometer *G*, Daniell element, rheocord *Rh*, back to the other electrode *t*, on the transverse surface. A key or shunt is introduced in the circuit, and the time of closing can be varied by moving the arms supporting the cups.

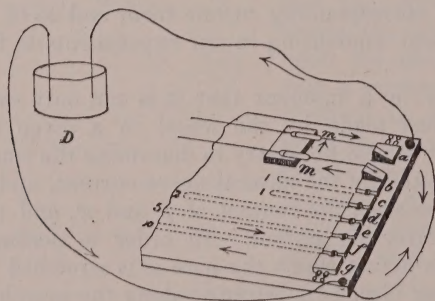
As the rapidity of the transmission of the negative variation in the nerve is determined from that of the rotation of the wheel, it becomes necessary to determine the latter. This is readily accomplished by counting the number of turns made by the marked thread connecting the wheel and the rotation apparatus and the number of rotations of the wheel corresponding to each turn of the thread, the latter being best done by so placing the point *p* that a sound is made each time it comes in contact with the wire *w*. The wheel being slowly rotated, the number of contacts between *p* and *w* are determined, corresponding to, say, five turns of the thread; this number being divided by five will then give the number corresponding to one turn, and so of the rapidity of rotation of the wheel, amounting in our experiments to five rotations in one second.

It will be seen in a moment that it is not only essential that the number of rotations made by the wheel in a given time should be known, but that it is also necessary to determine the time during which the needle is deflected by the natural nerve current, and the interval of time intervening between the contact of *p* and *w*, and the closing and opening of the diverting circuit. In order to accomplish this, the position of the box across which the wire *w* is stretched must be varied by sliding the brass piece supporting it along the periphery of the disk situated under the wheel, the distance through which it is moved by the screw being determined by means of the scale and vernier on the periphery of the disk, the scale being divided into hundredths, the vernier into thousandths. In order to determine the short interval of time during which the diverting circuit is closed, the pointer *p* is firmly clamped against the wire *w*, so that the wheel follows the motion of the screw. As soon as a deflection of the galvanometer needle, due to the diverting current, becomes apparent, the position of the slider is read off by the vernier, which we will call  $S'$ ; continuing to turn the wheel slowly onward, the needle will return to rest, and the position of the slider then, or  $S''$ , is read off, the rate of rotation of the wheel *R* being also known, the time required will be given by the equation  $t = (S' - S'')R$ .



Thus, suppose that  $S' = 0.9370$ ,  $S'' = 0.9254$ , and  $R = \frac{1}{5}$ th sec., then  $t$ , or the time during which the diverting circuit is closed, will amount to 0.00232 sec.,  $t = 0.0116 \times \frac{1}{5}$ th sec. = 0.00232 sec. In reading off  $S'$  and  $S''$  it must be remembered that each division of the scale corresponds to the  $\frac{1}{100}$ th of the distance traversed by the wheel during a single rotation, each division of the vernier to the  $\frac{1}{1000}$ th part, and that the numbers on the scale run in the opposite direction to that of the motion of the wheel. Further, that the time during which the diverting circuit is closed will vary according to the position of the mercury cups toward each other. The interval of time  $T$  elapsing between the contact of  $p$  and  $w$  and the contact of the pointers with the mercury cups, or the breaking of the contact with the same, is determined in the following manner. Let us suppose that the position of the slider be as in the preceding experiment at 0.9254 of the scale—that is, that the pointers at this instant leave the mercury cups. No modification of the natural electrical current by the stimulus can then be expected, since the diverting circuit remains open during an interval of time almost equal to that of a complete rotation of the wheel. Pushing, however, the slider along, and observing a deflection of the magnetic needle, the slider being at 0.9500, then  $0.9254 - 0.9500 = 0.0246 \times \frac{1}{5}$ th sec. = 0.0492 sec. will be the time required. In the same manner the time elapsing between the contact of  $p$  and  $w$ , and the contact of the pointers with the mercury cups, can be determined. It will be observed from Fig. 342 that the natural nerve current is compensated by means of the Daniell's element and rheocord, the magnetic needles

FIG. 343.



The rheocord. (SANDERSON.)

remaining at zero, except during the moment that the negative variation takes place, the nerve current being then diminished the magnetic needle will move in a direction due to the current from the Daniell's cell—that is, in a direction opposite to that which would be due to the nerve current acting alone. The object of so compensating the nerve current in the study of its negative variation by means of the differential rheotome is that the movement of the needle should always begin at the same point, viz., zero. It will be noticed, however, that the rheocord used—that of Du Bois-Reymond—differs in its form from that previously described, though the latter, for the present purpose,

might have been just as well used. The rheocord as made for the author by Elliot, of London (Fig. 343), consists of a long box, at the edge of which are stretched two platinum wires  $w w'$ , passing through the connected mercury cups  $m m$ , which can be pushed to the other end of the box along the scale graduated in millimetres at the side. When the mercury cups are directly in contact with the brass  $a$ , the resistance offered by the rheocord to the Daniell's circuit is practically nothing as compared with that offered by the nervous circuit, consequently the current from the Daniell's element simply passes through the rheocord back to the cell, none being diverted into the nervous circuit. If, however, the mercury cups be pushed away from the brass along the platinum wires, the wires offering a resistance, the amount indicated by the scale, 358 mm. = 1 ohm, and there being no passage for the current from one side of the rheocord to the other, except through the parts of the wires lying between the mercury cups and the brass, it follows that a proportional part of the total current from the Daniell's element is thrown into the nervous circuit.

If a greater amount of resistance is needed than that obtained by pushing the mercury cups through the whole length of the platinum wires, then the plugs lettered  $b, c, d, e, f, g$ , or numbered, can be drawn out, these being multiples of the resistance offered by the total length of the platinum wires traversed by the mercury cups, the amount of current thrown into the nervous circuit will be then proportionally increased. Thus, for example, if the plug 5, letter  $g$ , be withdrawn, then the amount of current thrown into the nerve will be five times as great as when the mercury cups were at the end of the wire, and so proportionally for the remaining plugs. In fact, the rheocord is a form of resistance box, such as already described. The stimulus made use of to excite the nerve in the study of the negative variation is the induction apparatus supplied by six to eight small Grove or Bunsen cells (B, Fig. 342), but it is better, according to Bernstein,<sup>1</sup> that the magnetic core of the primary spiral be withdrawn so that the magnetization and demagnetization of the same do not retard the course of the secondary induced current. Under these circumstances, the opening shock being more intense, but not lasting as long as the closing one, if the current used be strong, electrotonic currents appear, which modify the negative variation. Such currents, however, can be avoided by making the course of the two induced currents approximately equal, which Bernstein accomplished by intercalating in the primary circuit a short circuit consisting of two copper plates dipping in copper sulphate solution (not represented in Fig. 344). The significance of what has just been said with reference to the production of electrotonic currents, and of the modification of the negative variation by the same, will be appreciated when the subject of electrotonus has been considered.

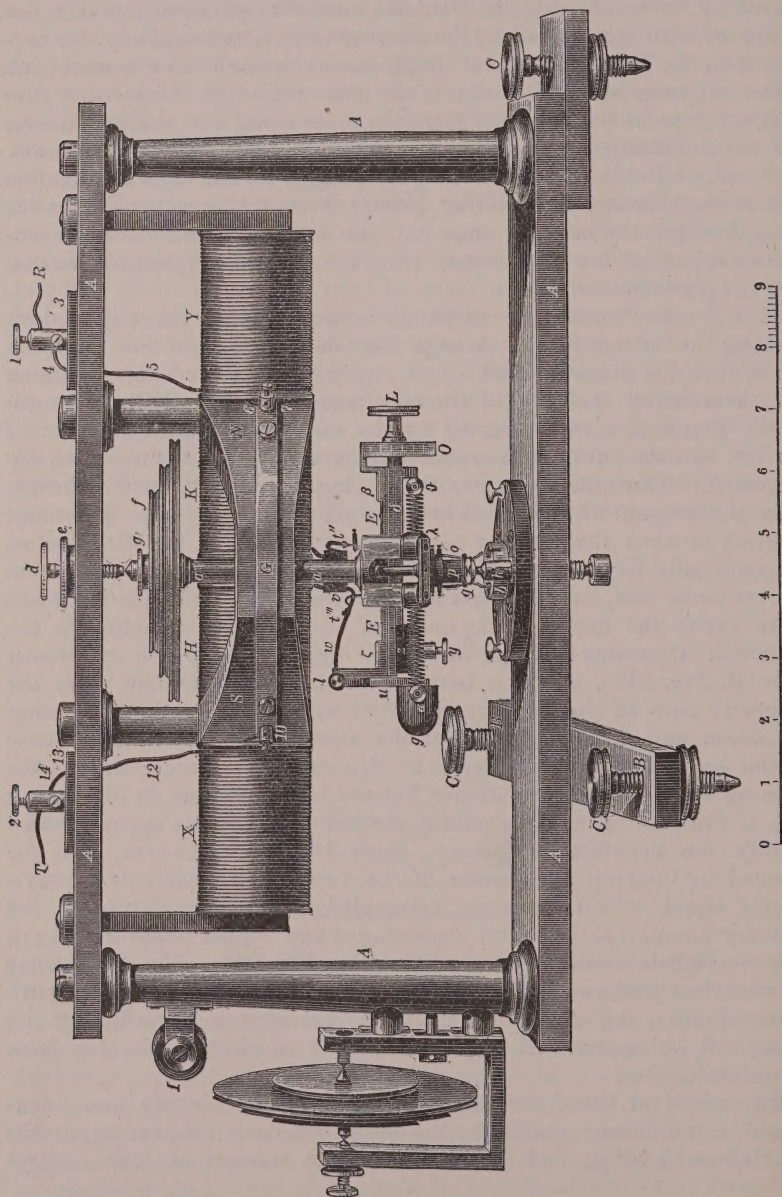
The wheel of the differential rheotome, as has already been mentioned, is uniformly rotated by the electromagnetic rotation apparatus of Helmholtz (Fig. 344, E). The latter consists of four electro-

<sup>1</sup> Op. cit., S. 16.



magnets, the two external ones ( $X Y$ ) immovable, the two internal ones ( $H K$ ) movable; the latter are fixed to the axis by their dissimilar poles, and are supplied by three Daniell's elements, the external ones by one. As the two internal magnets are repelled by the external ones, the axis is rotated, and with it the wheel ( $f$ ), through which it passes, and

FIG. 344.



Electromagnetic rotation apparatus.

around which passes the thread from the disk of the rheotome. Having described now the rheotome of Bernstein, with the accessories, and the manner in which it is used, let us consider how by means of it the rapidity, duration, etc., of the negative variation are determined. In order to determine the rapidity of the transmission of the negative variation, let us begin the experiment by so arranging the slider that contact is made between  $P$  and  $W$ , at division 1 of the scale at the moment that the diverting circuit is opened—that is, at the instant the pointers  $p^1 p^2$  leave the mercury cups  $c^1 c^2$ . As the time elapsing before the diverting current is again closed is then almost equal to one entire rotation of the wheel, no deviation of the magnetic needle occurs, since, though the nerve current be diminished, the needle will give no evidence of it, the diverting current not having been closed in time. Let us now push the slider along the scale to the division 2—that is, over the  $\frac{1}{100}$ th of the circumference, and suppose that the needle begins to be deflected through the commencing diminution of the nerve current, then, as the interval of time elapsing between the application of the stimulus to the nerve at  $a$  (Fig. 342), through the contact of  $P$  and  $W$ , and the beginning of the negative variation at  $b$ —that is, the time during which the negative variation is transmitted through the nerve from  $a$  to  $b$ —is the same interval of time during which the wheel moves from division 2 to 1, carrying the pointer from  $A$  to  $B$ , equal to  $0.01 \times \frac{1}{5}$  sec. or  $\frac{1}{500}$ th sec. ( $\frac{1}{5}$  sec. being the rate of rotation of the wheel), it follows that the negative variation must have travelled along the nerve from the point stimulated ( $a$ ), to the point from which the current was diverted ( $b$ ), a distance of 5 cm., or 2 inches, at the same rate, viz.,  $\frac{1}{500}$  sec. or on an average, according to Bernstein,<sup>1</sup> of about 25.8, 28.7 metres a second, the rate of propagation of the nerve force itself.

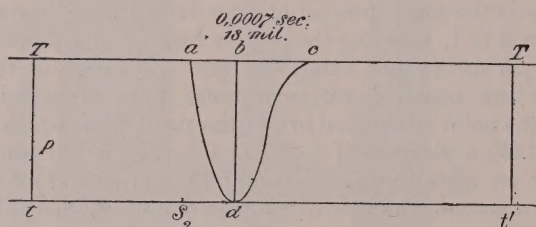
At first sight, as an objection to the conclusion just reached, it might be urged that an interval of time may elapse between the application of the stimulus and the beginning of the negative variation at the point stimulated. That no such latent period, so to speak, however exists, at least as determined by present means of investigation, can be shown by first stimulating the nerve at some distance from the diverting electrodes, and then near the latter, the difference in the time of the transmission of the negative variation depending upon the length of the nerve traversed. Although the phenomenon of the negative variation is a momentary one, it occupies a sufficiently large interval of time to be measurable by the rheotome. Thus, for example, suppose that when the negative variation begins the slider is at a position that we will call  $Se$ , and when it ends that the latter is at  $Sa$ , and the time of closing the nerve circuit be called  $t$ , and the rate of the rotation of the wheel  $R$ , then the formula  $(Se - Sa - t) R$  will give the duration of the negative variation, which Bernstein<sup>2</sup> finds, on an average, amounts to 0.0006759 sec.; or, let us suppose that the slider is at a position  $Se$ , when the negative variation ends, and that  $S'$  be the position of the slider at the moment of contact  $p$  and  $w$ , then  $(Se - S') R$  will be the interval of time elapsing between the moment of stimulation and the



end of the negative variation, while if by  $t$  we denote the time during which the nerve force is propagated from the spot stimulated to the first diverting electrode, then the formula  $Se-s' R-t$  will give the duration of the negative variation, which obtained by this method amounts, according to Bernstein,<sup>2</sup> to 0.0007026 sec., and which value does not differ very much from the value obtained by the preceding method. In observing the phenomenon of the negative variation, as just described, from its beginning to its end it cannot fail to be observed, if the slider be pushed very gradually along that it attains its maximum and minimum limits very gradually. Thus, suppose that when the slider is at 0.9555 the negative variation begins, it is not until the slider passes from 0.960 to 0.980 that the maximum intensity is attained, and until it has reached 0.0994 that it entirely disappears. In other words, the negative variation propagates itself in the form of a wave, and it remains for us now to explain how such a wave can be graphically represented, and its length estimated.

Let the abscissa  $t' T'$  (Fig. 345) represent the time of one entire rotation of the wheel, and the ordinate  $t T$  the deviation of the magnetic

FIG. 345.

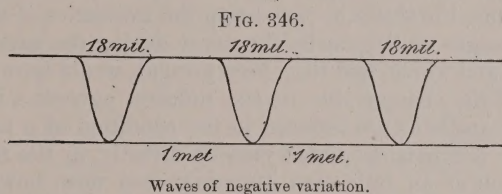


Graphic representation of distance and length of the negative variation.

needle due to the natural nerve current, then  $T T'$  will represent the condition of that nerve current during that time, supposing its intensity remains unaltered. Let us suppose, also, that at the moment ( $t$ ) the nerve is stimulated, the negative variation begins at  $a$ , then the period intervening between the application of the stimulus at  $t$  and the beginning of the negative variation at  $a$ —that is, the time during which the negative variation has travelled through the part of the nerve intervening between the stimulating and diverting electrodes—will be represented by  $t S_2$ ,  $S_2$  being the moment of the closing of the diverting circuit. Further, let us suppose that the negative variation beginning at  $a$ , attains a maximum at  $b$ , and disappears again at  $c$ , the slider having been pushed along, as already described; if the deviation of the magnetic needle occurring between the moments  $a$  and  $c$ , represented by ordinates drawn downward from  $T T'$ , then we will obtain a curve  $a d c$ , the graphic representation of the negative variation as it passes over a given portion of the nerve, and which, as may be seen, while falling suddenly, rises rather slowly again to the line  $T T'$ . It should be mentioned, with reference to this curve, that while, according to

<sup>1</sup> Op. cit., S. 25.

Bernstein,<sup>1</sup> its lowest point (*d*) may lie either above, on, or even below the abscissa line; according to Funke<sup>2</sup> the lowest part of the curve may reach the abscissa, but never falls below it. On account of the wave of the negative variation being due to that stimulus, which, in a nerve, gives rise to sensation, muscular contraction, etc., it may be called, as by Bernstein, the stimulus wave. Finally, if it be admitted that the duration of the negative variation represented in Fig. 367 by *ac*, be equal to 0.0006–0.0007 sec., and that the negative variation travels at the rate of 28 metres a second, evidently then the length of the wave *ac* will be equal to 0.0006–0.0007 of 28 metres=16–18 mm. Further, if it be supposed that while the negative variation travels at the rate of 28 metres a second, that during the same period of time the nerve be stimulated 28 times, then a nerve 28 metres long would exhibit at the end of the second 28 waves of negative variation, each wave being separated by an interval of 1 metre (Fig. 346). The exact



limits of the wave are readily determined by the rheotome, since, by employing a series of rotations, we get the effect of the summation of a series of stimuli, instead of that due to a single one. In the latter case the indications are not sufficiently delicate to define the beginning and end of the wave. While in the present state of our knowledge of the nervous system it may be premature to draw any very positive conclusion as to the nature of the negative variation, nevertheless, from what has just been learned by the rheotome, of the negative variation being produced by opening and closing periodical shocks following each other not too rapidly, of being propagated in the form of a wave, of having a definite duration, there can be but little doubt that the change undergone by the nerve during the negative variation is vibratory molecular in character similar to the propagation of water waves, of sound waves in air, of light waves in ether.

With this difference, however, that in the case of the negative variation wave coincidently with the vibratory motion of the nerve molecules, chemical modifications of the substance of the same are going on which are wanting during the propagation of sound and light waves. Further, the electrical condition of the nerve during its phase of negative variation becomes intelligible if we assume that every part of the longitudinal surface of the nerve becomes successively negative with reference to the preceding point that has just undergone the negative variation, and to the succeeding one still to undergo it. Such an electrical condition can be accounted for by supposing that during the

<sup>1</sup> Op. cit., S. 33.

<sup>2</sup> Physiologie, Band i. S. 509.

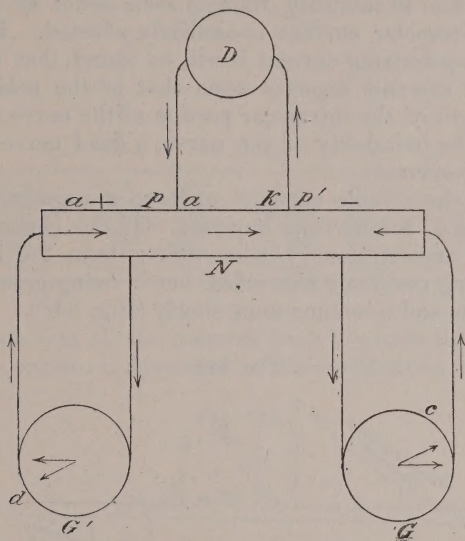


negative variation the electromotive force and the resistance are both diminished. As a matter of fact, the latter has been proved to be experimentally the case<sup>1</sup> and as a more perfect closure of the nerve circuit is then effected a partial current correspondingly weakened will pass through the diverting electrodes, while from the chemical changes going on in the active nerve it is a reasonable inference to suppose that its electromotive force is also modified. Finally, whatever view may be taken of the electrical condition of the nerve during the negative variation, or its cause, the conclusion seems unavoidable that the diminution of the natural nerve current during the activity of the nerve, its negative variation or stimulus wave whether produced by electrical, chemical, thermal, or mechanical stimuli, is that which excites the muscle to contract, the gland to secrete, the organ to feel.

Up to the present moment, in exciting the nerve by electrical stimuli we have made use of single or repeated induction shocks, and this not only for convenience' sake, but especially on account of the short duration of induced currents, the object in view being the avoidance of the consideration of the changes undergone by the nerve during the passage of a constant current, and which, had they been present, would have rendered the explanation of the changes due to the induced current a more difficult one. Such changes as are induced in the condition of a nerve through the passage of a constant current passing directly to the nerve without the intervention of an induction apparatus can now, however, be conveniently considered. Let us suppose, then, that *N* (Fig. 347) represents a nerve, and that through the deviation of the magnets of the galvanometers *GG'* we learn that the natural electrical nerve currents are present, passing from the longitudinal surface through the galvanometers to the transverse cut surface of the nerve, through the nerve to the longitudinal surface again in the direction indicated by the arrows. Let now the nerve *N* be stimulated through the non-polarizable electrodes *p p'* at a point intermediate between its ends, *b*, by means of a constant current, say, from a Daniell's element, and which we will hereafter designate as the polarizing current, the deflection of the galvanometer needles in the reverse direction toward zero will show that the natural electrical nerve currents have both been diminished, the negative variation travelling as already mentioned in both directions along the nerve from the point stimulated, and giving rise to a contraction of the muscle if the latter were still attached to one end of it. The negative variation lasting, however, as we have seen, but a very short time, having come and gone in the interval of the 0.0007 of a second is but a very transitory phenomenon; the magnetic needles should therefore at once return to the position they occupied before the deflection due to the diminution of the natural electrical nerve current. Such, however, is not the case, since, as shown by the deviation of the needles, the current passing through the galvanometer *G* is diminished (*c*), that through *G'* increased (*d*). It is evident, therefore, that the electrical condition of the nerve is not only modified temporarily by the momentary stimulus of the constant current, the negative variation,

but permanently also during the passage of the current through the nerve in the modification of its electrical condition in the manner just mentioned. It will be observed from an inspection of Fig. 347, that

FIG. 347.



Anelectrotonic and katelectrotonic currents.

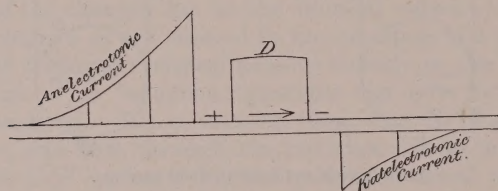
the polarizing current is direct—that is, as it passes through the nerve from the anode *a*, or positive pole, to the kathode *k*, or negative pole, it flows in the same direction as the nerve force itself. Now if it be assumed that the polarizing current develops outside of the electrodes *p p'*, a new current, the electrotonic current, having the same direction as itself, it is evident that the increasing or diminishing of the natural nerve current by the electrotonic current, according as the latter is flowing in the same or in the opposite direction, will account for the difference in the electrical condition of the nerve outside of the anode *a*, and kathode *k*, the former being positively, the latter negatively, electrified. Such being the case, we may call that part of the electrotonic current increasing the natural nerve current the anelectrotonic, that diminishing the same the katelectrotonic current, indicating the electrical conditions of the two currents respectively by the signs plus + and minus —. If now the position of the two electrodes *p p'* be reversed so that the polarizing current flows through the nerve in the opposite direction to that of the nerve force, then the anelectrotonic current will be developed at *p*, the katelectrotonic at *p'*, and the current passing through the galvanometer *G* will be increased, that through the galvanometer *G'* diminished. It will be observed, therefore, that the anelectrotonic and katelectrotonic condition just described will depend upon the fact of the polarizing current passing through the nerve in the direct or reverse direction. In either instance, when the polarizing



current is broken the natural nerve current previously diminished or increased is for a brief moment increased or diminished. While there can be no doubt as to the existence of the anelectrotonic or katelectrotonic currents, and that the same spread along the extrapolar portions of the nerve from the anode and kathode, respectively, with a gradual diminution in intensity, there is some doubt as to what extent if at all, the intrapolar current is similarly affected. By varying the strength of the polarizing current it will be found that the strength of the electrotonic currents depends upon that of the polarizing current and of the length of the intrapolar portion of the nerve exposed to the latter, and of the irritability of the nerve, a dead nerve not exhibiting the electrotonic current.

Finally, the electrotonic currents undergo a negative variation during the passage of the nervous impulse. Of the electrotonic currents developed, the anelectrotonic portion differs from the katelectrotonic, not only in being positively electrified, but in being greater and attaining its maximum and minimum more slowly (Fig. 348). Further, while

FIG. 348.



Graphic representation of anelectrotonic and katelectrotonic currents.

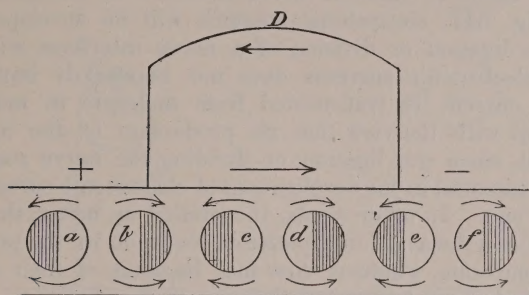
according to Du Bois-Reymond,<sup>1</sup> the electromotive force of the electrotonic current amounts to 0.5 of a Daniell, that of the katelectrotonic current 0.05 D. While the electrotonic currents just described are without doubt produced by the polarizing current, there is still some difference of opinion among physiologists as to whether these currents are due to some especial modification of the electromotive condition of the nerve, which, like the negative variation, is transmitted from the point stimulated through the nerve, from molecule to molecule, or are due to the direct effect of the polarizing current through an escape of the latter, from the electrodes along the extra-polar portions of the nerve. The grounds which induced Du Bois-Reymond<sup>2</sup> to suggest the former or molecular view are, for example, the alleged absence of electrotonic currents, if the nerve be ligated at a point intervening between the polarizing and diverting electrodes, or if it be divided and the two cut ends subsequently brought in close contact, or if a moistened thread be substituted for the nerve in the experiment described at p. 609, and illustrated by Fig. 347, which ought not to be the case if the electrotonic current is simply an escape of the polarizing one. Du Bois-Reymond, therefore, considers, according to his view of the nerve

<sup>1</sup> Gesammt. Abhandl., ii, S. 260.

<sup>2</sup> Untersuchungen über Thierische Electricität, Berlin, 1848-60.

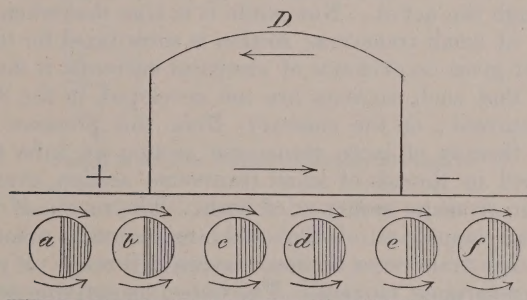
consisting of electromotive molecules (Fig. 349), that the effect of the polarizing current is so to modify the position of these molecules that their opposite poles are brought to face each other as in Fig. 350, the

FIG. 349.



effect being then that all the currents have the same direction—that is, an electrotonic current is developed. The modification in the position of

FIG. 350.



Modification of molecular conditions of nerve by passage of constant current.

the molecules *a*, *c*, *e*, the direction of whose currents is opposed to that of the polarizing current, supposing the latter to be direct, as in Fig. 349, is attributed to an electrolysis, similar to that produced by transmitting an electric current through water, with this difference, however, that the electrifying influence extends itself beyond the electrodes, without which assumption it would be impossible to explain the existence of the anelectrotonic and katelectrotonic currents. Further, in order to account for the strength of the electrotonic current depending upon that of the polarizing one, Du Bois-Reymond supposes that of the numerous molecules of which the nerve consists either with a weak current only a few of them are turned, or that all are turned, but only more or less imperfectly. On the other hand, it is argued by Matteuci,<sup>1</sup> Gruenhagen,<sup>2</sup> and Hermann,<sup>3</sup> that the electrotonic currents can only be produced

<sup>1</sup> Comptes Rendus, 1863, lvi. p. 760; 1867, lxx. pp. 151, 194, 884; 1868, lxxi. p. 580.

<sup>2</sup> Funke: Physiologie, Zweiter Band i. S. 495.

<sup>3</sup> Physiologie, Zweiter Band, S. 174.

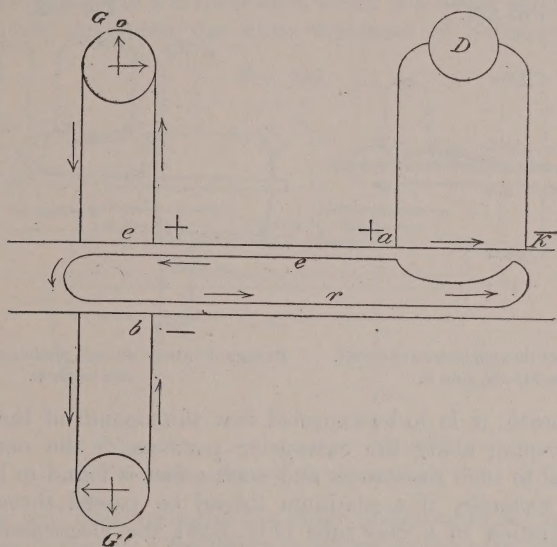


by electrical ones and not by other nerve stimulants, such as heat, chemical agents, etc., which ought not to be the case, if the electrotonic currents be due to an essential modification of the electrical condition of the nerve molecules; further, that if a moistened thread so prepared as really to resemble nerve structure be substituted for the nerve of Fig. 347, electrotonic currents will be developed, and the fact that the ligation or division of a nerve interferes with the production of electrotonic currents does not necessarily imply that the electrotonic current is transmitted from molecule to molecule, and is inconsistent with the view that its production is due to the polarizing current, since the ligation or dividing the nerve may destroy a portion of it essential in the development of electrotonic currents through a polarizing one. In other words, the vitality, or, better, the continuity of the nerve may be as an indispensable condition in the production of electrotonic currents, whatever view may be taken of their origin.

It has already been mentioned that one of the objections to the view of the electrotonic current being the direct effect of the polarizing one, is the fact of a moistened silk thread, when traversed by a current, not exhibiting, like a nerve, electrotonic currents, which ought to be the case if the phenomenon is due simply to the escape of the electrical current, and not to a physiological modification generated and transmitted through the nerve. Now while it is true that when a moistened silk thread of small transverse section is substituted for the nerve, the galvanometer gives no evidence of electrical currents, it does not, however, follow that such currents are not developed in the thread by the polarizing current; on the contrary, from the presence of electrical currents in threads of large transverse section we infer that they are also developed in threads of small transverse section, even though the galvanometer gives no evidence of such. The reason of this becomes clear from an inspection of Fig. 351, representing a moistened silk thread of large transverse section traversed through a portion of its extent by a polarizing current. The latter, on arriving at the positive pole or anode (*a*) divides into two branches, one of which returns at once through the intrapolar portion of the nerve to the negative pole or kathode (*k*), and so back to the Daniell's element; the other, on the contrary, spreads outwardly from the anode as the leaving current (*e*), and after traversing the diverting circuit, and deflecting the galvanometer (*G*), returns as the returning current (*r*) to the kathode, and so to the Daniell's element. It will be observed, however, from Fig. 351, that according as the diverting electrodes *G* *G'* are disposed with reference to the leaving or returning currents, they change their sign as at *c* *b*, the diverting electrode *c* lying nearest to the stimulating electrode *a*, assuming the electrical condition corresponding to that electrode, that at *b* the electrical condition corresponding to *K*. Now it is obvious, that if the silk thread have a very small transverse section, the leaving or returning currents lie then so closely together, that in being diverted into the galvanometer, they neutralize each other, and exercise no influence upon the magnetic needle. It becomes perfectly clear, therefore, why moist conductors of small transverse section traversed by a polarizing current exhibit no electrical currents

in the extrapolar portions of the nerve. Now a nerve differs essentially from such a moist conductor not only in exhibiting electrotonic currents when traversed by a polarizing one, even though presenting a small transverse section, but also that these currents have the same

FIG. 351.



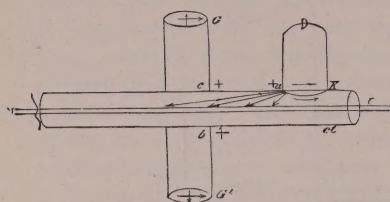
Passage of electrical current in moistened silk thread.

sign whether the diverting electrodes be placed upon the same side of the nerve as the stimulating electrodes, or the opposite side, as at  $c b$  (Fig. 352). No such difference between a nerve and a moist conductor, however, is apparent if the latter is so made as to resemble a nerve in its structure—that is, consists of a central axis, which is a better conductor than the surrounding envelope, as, for example, when a thread ( $t$ , Fig. 352) moistened with strong salt solution, is surrounded by a porous clay tube ( $ct$ ) whose walls have been previously soaked in distilled water, or when a stick of amalgamated zinc is surrounded by a similar tube soaked in zinc sulphate solution. The leaving currents will, in such a conductor, have the same direction, owing to the fact of the substance coating the axis being a better conductor than the envelope, while the return currents all running in the better conducting axis, the current will also have the same sign, however the diverting electrodes be placed upon the surface of the nerve. Further, the electrotonic currents so developed resemble those of a nerve in being entirely dependent upon the polarizing current, of the length of the nerve traversed by the latter, etc. If, now, such a heterogeneous conductor be divided in the middle, and the cut ends be joined by a homogeneous moist conductor like that already described, no electrotonic currents will appear, for the reasons already given. It is in this way, probably, that the ligation or the crushing of the nerve



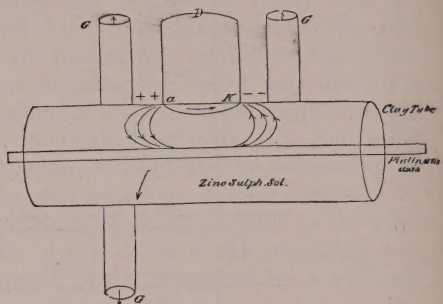
interferes with the development of such currents, the nerve, after death, being changed from a heterogeneous to a homogeneous conductor. Further, as the escape of the polarizing current, either in the nerve or the heterogeneous conductor, appears to be due to the resistance developed through the inner polarization set up between the core

FIG. 352.



Passage of current through moistened thread, enclosed in clay tube *et.*

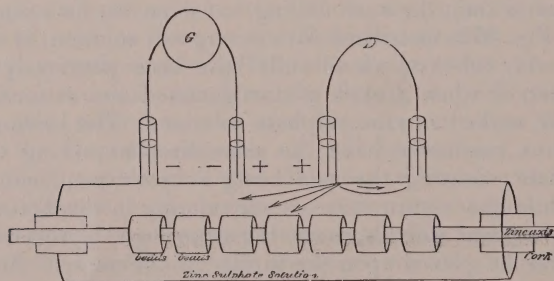
FIG. 353.



Passage of current through platinum, surrounded by zinc sulphate.

and the sheath, it is to be expected that the amount of the polarizing current escaping along the extrapolar portions of the nerve will be proportional to such resistance, and such a fact is found to be the case. Thus, for example, if a platinum thread be passed through a zinc sulphate solution in a clay tube (Fig. 353), the electrotonic currents developed will be much greater than if the axis consisted of amalgamated zinc. Indeed, as we have already seen, amalgamated zinc and zinc sulphate solution are so homogeneous, that we use them to make non-polarizable electrodes. An interesting illustration of the difference in effect as regards the development of electrotonic currents due to the

FIG. 354.



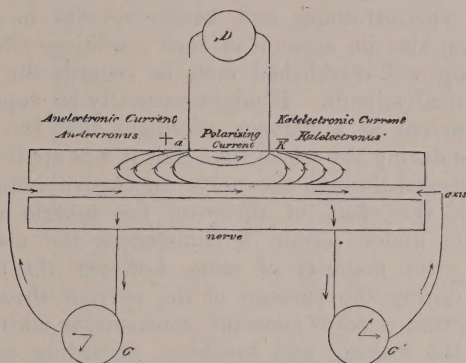
Passage of current through heterogeneous conductor.

conductor being homogeneous or heterogeneous can be readily shown by the following simple apparatus (Fig. 354), which consists of a glass tube through which passes an axis of amalgamated zinc.

If the tube be filled with zinc sulphate solution, the galvanometer gives no evidence of electrotonic currents; but if a number of little

glass beads be run along the axis, the spaces between the beads corresponding, let us say, to the nodes of Ranvier in the nerve, the galvanometer will be at once deflected, the conductor having been converted from a homogeneous into a heterogeneous one. The different facts just referred to, established by Funke, Gruenhagen, Hermann, etc., all go to show that the living nerve is a heterogeneous conductor, consisting (Fig. 355) of a central axis, which is a better conductor than its surrounding envelopes, the white substance of Schwann, and the

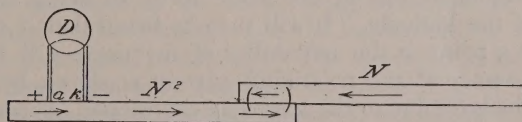
FIG. 355.



Passage of current through nerve.

neurilemma, and that, owing to the inner polarization set up between the axis and its sheath, a resistance is offered to the polarizing current, hence its escape along the extrapolar portions of the nerve; the latter, owing to the resistance being gradually diminished, at last passes into the axis, and thence by the kathode back to the Daniell's element. Finally, the electrotonic current so developed, in increasing or diminishing the neutral nerve current, gives rise to the anelectrotonic and katelectrotonic currents respectively. While in the present state of physiological knowledge it may appear premature to accept, without reserve, the view that attributes the electrotonic current to the escape of the polarizing one, nevertheless, it must be admitted that the facts, so far as they have been established, are better explained by this view than by any other yet advanced. Finally, if a nerve (*N*, Fig. 356) be placed upon another (*N* 2), the latter exhibiting an electrotonic

FIG. 356.



Secondary electrotonic current.

current, a secondary electrotonic current will be developed in the former opposite in direction to that of the current producing it as represented in Fig. 356, the current being closed by the ends of the nerve lying in

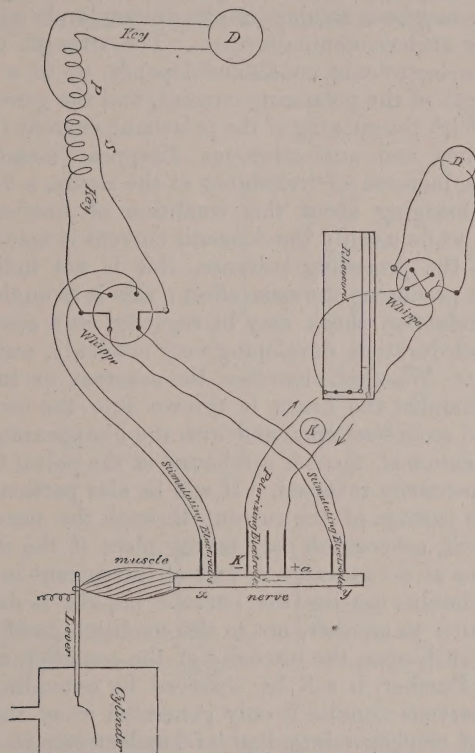


contact with each other. It is an interesting fact, in this connection, that when a nerve is traversed by a polarizing current not only do the anodal and kathodal portions of the nerve differ in the presence of anelectrotonic and katelectronic currents, but also in exhibiting the conditions of anelectrotonus and katelectrotonus (Fig. 355), the former being one of diminished, the latter of increased, excitability and conductivity respectively. The anelectrotonic and katelectrotonic conditions are not only interesting from being intimately connected in so many respects with the anelectrotonic and katelectrotonic currents, the latter, indeed, being so named for this reason by Du Bois-Reymond, the phenomena of anelectrotonus and katelectrotonus having been discovered first, but also on account of such conditions offering an explanation of certain well-established facts as regards the excitability of nerves by electrical stimuli. It might naturally be supposed in using the constant current as a nervous stimulant that the current would excite the nerve during the whole time that it was applied, that so long as the current passed through the nerve successive impulses would be generated, with the effect of throwing the muscle into a kind of tetanus. While under certain circumstances the above does take place, in the great majority of cases, however, the muscle remains entirely quiet during the passage of the current through the nerve, provided the current remains constant, contractions taking place at the making, or at the making and breaking, according as we shall see presently, to the strength and direction of the current. It may be said, therefore, as a general rule, that, during the passage of a constant current the muscle remains at rest. Nevertheless, as we have just seen, in the absence of any muscular contraction, the nerve is profoundly modified during the passage of a constant current by the development at the anode and kathode of the anelectrotonic current and anelectrotonic condition of the katelectrotonic current and katelectrotonic condition, respectively, conditions intimately connected with the peculiarities just referred to as regards the muscular contraction brought about by the opening and closing of the electrical circuit.

Before considering, however, these relations, let us first show how the difference already mentioned in the excitability of the nerve at the anode and kathode, respectively, can be demonstrated. With this object, we will dispose the necessary apparatus, as represented in Fig. 357, and let us suppose, first, that the polarizing current thrown into the nerve by the opening of the key, and whose strength is regulated by the rheocord, is direct, descending—that is, traverses the nerve in the same direction as that of the nerve force—*a* being, therefore, the anode, and *K* the kathode. It will then be found that if the nerve be stimulated at a point *x* the irritability of the nerve will be increased during the passage of the polarizing current as shown by the greater elevation of the lever due to the muscular contraction, as compared with the average elevation previously determined with the same stimulus, but in the absence of the polarizing current. On the other hand, if the nerve be stimulated at a point *y* the irritability of the nerve will be found to be diminished. That it is not the distance of the point *y* from the muscle, as compared with that of *x*, to which the diminution in

irritability at  $y$  is due is shown, apart from what has already been said with reference to the stimulation of a nerve at different distances from the muscle, by reversing the polarizing current by means of the whippe, so that it becomes an inverse ascending one, the anode being then, therefore, nearer the muscle than the kathode; even then the irritability

FIG. 357.



Disposal of apparatus to demonstrate electrotonus.

of the nerve at  $x$  is diminished, and, with certain qualifications, to be mentioned presently, that at  $y$  is increased. In this way, then, it is shown that during the passage of a constant current the irritability of the nerve at the kathode is increased and at the anode diminished, the change in the condition of the nerve being described as that of katelectrotonus and anelectrotonus, or as the katelectrotonic increase, and anelectrotonic decrease of irritability. The condition of katelectrotonus and anelectrotonus not only modifies the irritability of the nerve as regards the originating of nervous impulses, but appears also to influence their propagation—at least it may be said that the condition of anelectrotonus offers an obstacle to the passage of a nervous impulse. The condition of katelectrotonus and anelectrotonus not only spreads out along the extrapolar portions of the nerve, but, unlike the katelectrotonic and anelectrotonic currents, extends also into the intrapolar

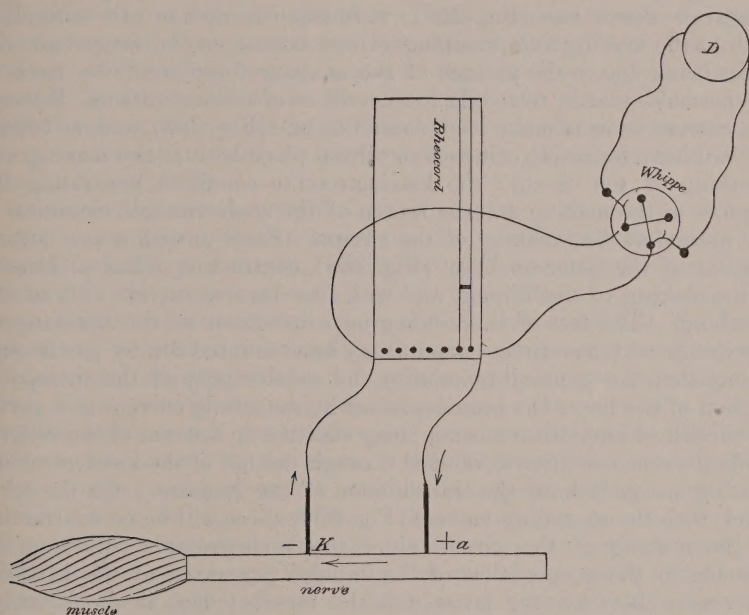


portion, the point where they merge into each other—that is, where the irritability is unchanged—being known as the neutral or indifferent point. The position of the latter varies somewhat, according to the strength of the current, with a strong current approaching the kathode, with a weak one the anode. While the katelectrotonic increase and anelectrotonic decrease of irritability reach a maximum shortly after the making of the polarizing current, and then gradually diminish, the katelectrotonic increase, attains its maximum and minimum limits sooner than the anelectrotonic decrease. The strength of the katelectrotonic and anelectrotonic conditions depends, up to a certain limit, upon the strength of the polarizing current, and the general irritability of the nerve. With the opening of the polarizing current the phenomena of katelectrotonus and anelectrotonus disappear momentarily, however, there is an increase of irritability at the anode, a decrease at the kathode. In bringing about this condition of katelectrotonus and anelectrotonus, while usually the constant current is made use of as the stimulus, as in the preceding instance, this is not indispensable, an induced current producing the same effect; this is as might be expected, since a single induction shock may be regarded as a constant current, but of very short duration, developing very suddenly, and disappearing more gradually. Whether, therefore, the constant or induced current be used as a stimulus the nerve is thrown into the condition of katelectrotonus and anelectrotonus, and with the disappearance of the current, as just mentioned, there is a rebound at the poles, their condition being then momentarily reversed. It will be also particularly observed that during the passage of the current through the nerve the muscle remains quiescent, contraction only taking place if the strength of the current varies, or at the entrance or exit of the current into or from the nerve. The stimulus causing the nervous impulse is due to a change from one condition to another, not to the condition itself, the effect not depending so much upon the intensity of the condition as on variation of the same. Further, it will be observed by extending our experiments, that a nervous impulse is only generated when the nerve passes from its normal condition into that of katelectrotonus, or that of increased irritability, and diminished electrical potential, or passes from the condition of anelectrotonus, that of diminished irritability and increased electrical potential, back to the normal condition, the latter normal condition being then, relatively at least, one of katelectrotonus, as compared with the immediately preceding anelectrotonic condition. As might be expected, however, the passage of the nerve from the anelectrotonic to the normal condition is far less effective as a generator of nervous impulses than that from the normal to the katelectrotonic condition, since the return from the anelectrotonic to the normal condition is a gradual, not a sudden one, and the change acts as a stimulus, at best only relatively. Hence, with induced currents at least, usually the muscular contraction takes place only at the closing, not at the opening of the current.

Let us now modify the arrangement of the apparatus just used so that (Fig. 358) by means of the rheocord we can modify the strength of the constant current, and, by the whippe, reverse the direction through

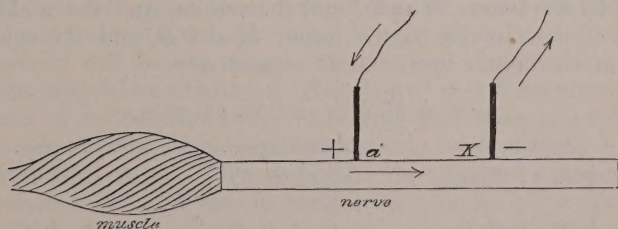
which it traverses the nerve, and let us suppose first that the current is a weak one, descending direct at the moment of stimulation—that is, at the making of the circuit, the muscle will contract, remaining quiet, however, during the passage of the current and also at the breaking of the same. Let us now reverse the direction of the current, so that it becomes an inverse ascending one (Fig. 359), then, as before, the muscle will contract only at the making of the circuit. The effect in both instances being the same, can be accounted for by supposing the kat-

FIG. 358.



electrotonic condition acts as a stimulus, the impulse generated at the kathode in the case of the inverse current being still effective, even though the distance of the kathode from the muscle is increased. Since,

FIG. 359.



however, the latter impulse generated at the kathode has to traverse the anelectrotonic portion of the nerve ( $a$ ), which, as it will be remembered, offers an obstacle to the propagation of the impulse, the



muscular contraction due to the making of the inverse current will be less than that due to the making of the direct one. That no contraction takes place at the breaking of the circuit with either the direct or inverse currents is to be expected, since, with the breaking of the direct current, the kathode offers an obstacle, having become momentarily the anode, to the propagation of the impulse due to the weak katelectrotonic condition momentarily developed at the anode, and, with the breaking of the inverse current, the fall at the anode from anelectrotonus to the normal is too slight to generate an impulse. Let us now intensify the current and reverse its direction by the whippe, so that it is again a direct one (Fig. 358): muscular contraction will take place both at the making and breaking of the circuit, in the latter case the effect being due to the passage of the anelectrotonic condition back to the normal—that is, relatively to a condition of katelectrotonus. Reverse the current so as to make it an ascending one (Fig. 359), and, as before, we will have muscular contraction taking place both at the making and breaking of the circuit: the katelectrotonic condition generating the impulse at the making and the return of the anelectrotonic condition to the normal at the breaking of the circuit. Finally, with a very strong current, if the latter be direct (Fig. 358), contraction takes place only at the making of the circuit, and with the inverse current only at the breaking. The fact of there being no contraction at the breaking of the circuit with the direct current may be accounted for by partly supposing that the general irritability and conductivity of the intrapolar portion of the nerve has been depressed by the strong current and partly by the fall of anelectrotonus not being effective on account of the relative anelectrotonic condition developed through the fall of the katelectrotonic offering an obstacle to the transmission of the impulse. On the other hand, with the ascending current (Fig. 359) there will be no contraction at the making of the circuit, since the anelectrotonic condition, an obstacle to the propagation of the impulse generated at the kathode, intervenes between the latter and the muscle; but, at the breaking of the circuit, the fall of the anelectrotonus to the normal relatively katelectrotonus will generate an impulse, since no obstacle intervenes then between the point of stimulation and the muscle, and the latter will contract. The above facts, established among others by Pfaff, Ritter, and Pflüger, may be summarized as a law of muscular contraction, under the following formula, in which the direct and inverse currents are indicated by the letters *D* and *I* and the arrows, and the making and breaking of the circuits by the letters *M* and *B*, and the contraction and rest of the muscle by *C* and *R* respectively.

## LAW OF MUSCULAR CONTRACTION.

|          | Weak current.      | Medium current. | Strong current. |
|----------|--------------------|-----------------|-----------------|
| <i>D</i> | $\vee M C, B R,$   | $M C, B C,$     | $M C, B R,$     |
| <i>I</i> | $\wedge M C, B R,$ | $M C, B C,$     | $M R, B C,$     |

The above law can be readily remembered, and the facts explained, if it be admitted, that muscular contraction only takes place when there

is a rise of katelectrotonus or a fall of anelectrotonus (relative katelectrotonus); but not by the rise of anelectrotonus or fall of katelectrotonus (relative anelectrotonus).

In concluding the subject of electrotonus one cannot but be impressed with the significance of the fact of the katelectrotonic condition, that generating the nervous impulse, being situated at that electrode whose electrical condition is diminished, when it is remembered that the propagation of the nervous impulse or the negative variation is also characterized by a diminution in electrical condition. These facts taken together at once suggest the idea of nerve force not being identical with electricity as once thought,<sup>1</sup> but of being correlated with the latter in some manner, the appearance of the one depending upon the disappearance of the other, or the absence of the one favoring the development of the other, and while this view cannot at present be accepted without reserve, to say the least it is certainly a plausible one and deserves consideration, being in harmony with the general doctrine of the conservation of force.

In concluding our account of nerve physiology it remains for us now to say a few words with reference to the conditions influencing the general irritability of nerves, which for convenience' sake have been reserved for the present moment, such as the influence exerted by the distance from the muscle of the point of the nerve stimulated, the duration of and number of the stimuli, the temperature and blood supply, the functional activity, severance from the central nervous system, etc. Thus, if two pairs of electrodes are placed upon the nerve of a freshly prepared nerve muscle preparation, one pair near the muscle, the other pair near the cut end of the nerve, it will be found that the muscular contraction is greater when the stimulus is applied through the latter pair than when through the former. This result can be accounted for either on the supposition that the nervous impulse gathers strength, avalanche-like, as it travels from the cut end of the nerve toward the muscle, or that the central end of the nerve is more irritable than the distal end—that is, that that portion of the nerve generates a longer nervous impulse when stimulated. The latter view is the most probable one, since the negative variation following in the steps of the nervous impulse exhibits no such avalanche-like increase as it progresses wave-like from the point stimulated to the muscle. It has been shown by König<sup>2</sup> that the constant current if used as a stimulus must last at least the 0.0015 second to produce a nervous impulse, and by Kroniker and Stirling,<sup>3</sup> that inductive shocks even if repeated as rapidly as 2200 times a second will throw a muscle into tetanus. In this connection it is an interesting fact according to Helmholtz,<sup>4</sup> that if maximum induction shocks be thrown into a nerve following each other at a rate of less than the  $\frac{1}{600}$ th of a second, half the shocks will produce no effect, the muscle being devoid of irritability for the  $\frac{1}{600}$ th of a second subsequent to each shock. A rise in temperature, say to 45° C. (113° F.),

<sup>1</sup> According to Haller. *Elementa Physiologiae*, t. iv. pp. 357, 373, the mathematician Hansen was the first to suggest that nerve force and electricity are identical. His views were not, however, published until after his death, appearing first in his "Novi profectus in historia electricitates," according to Du Bois-Reymond, *Untersuchungen*, ii. 1, S. 211.

<sup>2</sup> Wien Sitz. Bericht, lxii. (1870).

<sup>4</sup> Berlin Monats. Bericht, 1854.

<sup>3</sup> Archiv Anat. u. Phys., 1878, S. 1.



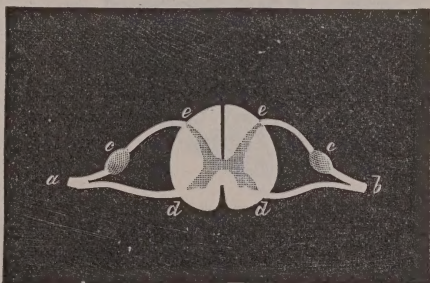
in the case of the frog's nerve favors the development of nerve irritability; the activity of the molecular processes being increased, nervous impulses are generated more readily by stimuli, and the muscular contractions are proportionately greater. On the other hand, the application of cold benumbs the nervous system, diminishes nervous irritability, the latter disappearing altogether if the temperature be reduced to  $0^{\circ}$  C. ( $32^{\circ}$  F.). Judging from what we shall learn hereafter from the analogous case of muscle there can be little doubt that the irritability of a nerve depends upon a full supply of oxygenated blood and that through prolonged use the nerve becomes exhausted. Finally, if a nerve be divided in the living body or even out of it, it will be observed that at the peripheral end of the cut nerve the irritability at first slightly increases, then diminishes, and finally disappears, the changes in the irritability advancing from the cut end of the nerve toward the muscle. Coincidentally with the changes in the irritability of the nerve just mentioned, a degeneration is set up in the substance of Schwann and the axis-cylinder extending to the terminal filaments, involving even their endings in the motor plates. A similar degeneration may extend also centripetally from the cut end, but not beyond the first node of Ranvier. Beyond this point the nerve is usually found normal.

## CHAPTER XL.

### THE SPINAL CORD, ITS STRUCTURE AND FUNCTIONS AS A CONDUCTOR OF MOTOR AND SENSORY IMPULSES.

THE spinal cord lying in the vertebral canal, enveloped within its membranes, extends as a cylindrical cord of from fifteen to eighteen inches in length from the medulla oblongata, with which it is continuous, at the level of the occipital foramen to the lower part of the first lumbar vertebra. It weighs about one and one-half ounces. If a transverse section of the cord be made, it will be observed (Fig. 360) that it consists of white matter externally, and of gray matter internally, the latter being found in the greatest amount opposite the cervical and lumbar enlargements, the origin of the large nerves. The gray matter is disposed as two crescents, placed back to back, somewhat in the form of the letter H, the anterior portion, the widest, being known as the anterior cornu, the posterior portion, the largest, as the posterior cornu, the middle connecting portion the gray commissure. The latter is often subdivided into the interior and posterior gray commissures by its central canal, which, as we shall see hereafter, is the remnant of the primitive neural canal. This peculiar arrangement of the gray matter within the spinal cord serves conveniently to subdivide the white portions of the cord into the anterior, lateral, and posterior columns. The anterior columns are made up by that part of the white matter of the cord lying between the anterior median fissure and the anterior cornu. It will be observed, however, that, as the anterior median fissure does not extend into the anterior gray commissure, a band of white matter, the white commissure, intervening, the anterior columns run into each other, and that, as the anterior cornu do not extend to the outer edge of the cord, the anterior columns pass into the lateral ones, lying between the two crescents. On the other hand, the posterior median fissure extending down to the posterior gray commissure, and the posterior cornu of the gray matter to the inner edge of the cord, the posterior columns lying between them are completely separated from the lateral columns, and from each other. In certain regions of the cord each posterior column is further sub-

FIG 360



Transverse section of the spinal cord. *a, b.* Spinal nerves of right and left sides. *d.* Origin of anterior root. *e.* Origin of posterior root. *c.* Ganglion of posterior root. (DALTON.)



divided by a rather obscure fissure into two sub-columns, the one, the posterior median column, lying immediately next to the posterior median fissure, often called the column of Goll, also the inner root zone of Charcot, the other the posterior external column, or the column of Burdach, or the outer root zone of Charcot. The white matter of

the spinal cord constituting its columns, as just described, consists principally of medullated nerve fibres, in which, however, a neurilemma and nodes of Ranvier are absent.

The course of these fibres through the columns is generally in a longitudinal direction, with the exception of such of them as pass transversely and decussating through the white commissure, or from the roots of the spinal nerves, and from the gray matter of the cord into the columns, the latter having a transverse or oblique direction. If the white matter of the cord be viewed in transverse sections with the microscope, the nerve fibres will then appear like small circles of different sizes (Fig. 361), with a rounded dot in the centre, the latter, or the axis-cylinder, being very distinct if the preparation be stained with carmine, while between groups of these nerve fibres fine septa of connective tissue may

Transverse section through the under half of the human cord. *a*. Central canal. *b*. Anterior. *c*. Posterior fissure. *d*. Anterior cornu, with large ganglion cells. *e*. Posterior cornu with smaller. *f*. Anterior white commissure. *g*. Sustentacular substance around the central canal. *h*. Posterior gray commissure. *i*. Bundles of the anterior, and *k* of the posterior spinal nerve roots. *l*. Anterior. *m*. Lateral. *n*. Posterior column. (After DEITERS.)

also be observed supporting delicate bloodvessels. The gray matter of the cord consists of a supporting connective tissue, the neuroglia of Virchow, composed of a fine network of round and large branched cells, imbedded in a homogeneous matrix, which, from being particularly abundant at the sides of the posterior cornu, is there known as the gelatinous substance of Rolando, of bloodvessels derived from the anterior median posterior root, and central vessels, of nerve cells, and nerve fibres.

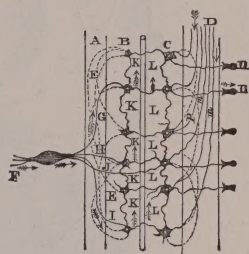
The cells in the gray matter of the cord are of two kinds, large multipolar cells (Fig. 361, *d*), such as are found in the anterior cornu, and small spindle-shaped cells (*e*) in the posterior cornu. Large multipolar cells are also found principally in the lower part of the dorsal region of the cord, behind the gray commissure, and on the inner surface of the posterior cornu, constituting the posterior vesicular column of Clarke. The gray matter of the cord consists also, or, rather, is traversed by innumerable delicate, non-medullated nerve fibres, which, in some instances, are undoubtedly continuations of the

poles or tails of the cells just mentioned, and which pass either into the roots of the spinal nerves or into the columns. On account, however, of the manner in which the sections are made necessarily, in many cases it is impossible to say anything positively as to either the origin or termination of such nerve fibres. Comparison of sections made, however, both in a longitudinal and in a transverse direction, leads to the supposition that all such non-medullated nerve fibres, or axis-cylinders, found in the gray matter of the cord, originate in either encephalic or spinal cells, and directly or indirectly, through spinal nerves, terminate in muscle, gland, or sensory organ. What has been positively learned by such methods of investigation as to the origin and course of these fibres may be briefly summed up as follows. The ultimate nerve fibres

of the anterior roots of the spinal nerves pass directly into the axis-cylinder like prolongations of the cells of the anterior cornu of the gray matter. The gray network produced through the repeated branching of these cellular prolongations gives rise to broad fibres, some of which, passing through the white commissure, ascend in the anterior column of the opposite side of the cord, while others (Fig. 362) passing into the antero-lateral columns of the same side, ascend to the medulla oblongata, where a greater proportion decussating with corresponding fibres from the antero-lateral column of the opposite side, pass thence through the pons Varolii and lower portion of the crus cerebri to the corpus striatum at the base of the brain. It appears, therefore (Fig. 363), that there are continuous tracts from the corpus striatum of one side of the brain through the crus, pons, medulla, through the antero-lateral column to the anterior roots of the spinal nerves emanating from the opposite side of the cord. The fibres from the posterior roots of the spinal nerves, after entering the cord, apparently separate (Fig. 362),

some ascending, others descending in the posterior columns, while others pass into the posterior cornu, and, after there dividing, terminate in a network of gray matter, by which they are indirectly connected with the cells of the posterior cornu. It will be observed that, while the fibres of the anterior root pass directly into the cells of the anterior cornu, those of the posterior root pass only indirectly into the cells of the posterior cornu, being connected with the latter by the intermediate network just mentioned. As fibres have also been satisfactorily demonstrated connecting the gray matter of the anterior and posterior cornu of the same side of the cord, and the cells of the anterior and posterior cornu of one side of the cord with those of the other, the latter fibres passing in front of and behind the central canal, it is evident that the fibres of the posterior roots of the spinal nerves entering the

FIG. 362.



A. Posterior column. B. Posterior horn of gray matter. C. Anterior horn of gray matter. D. Anterior lateral column. E. Loop-fibres of the posterior column proper. F. A posterior nerve-root. G. Ascending fasciculus of this root. H. Direct fasciculus. I. Descending fasciculus. J. Reflex motor root. K. Chain of sensory cells. L. Chain of motor cells. M. Encephalic fibres of the anterior columns. N. Anterior nerve-roots. O. Loop-fibres of the anterior roots. (CARPENTER.)



posterior cornu on one side of the cord are indirectly connected with the posterior cornu of the opposite side; and, as fibres have also been demonstrated passing upward in the gray matter of the cord, and

FIG. 363.

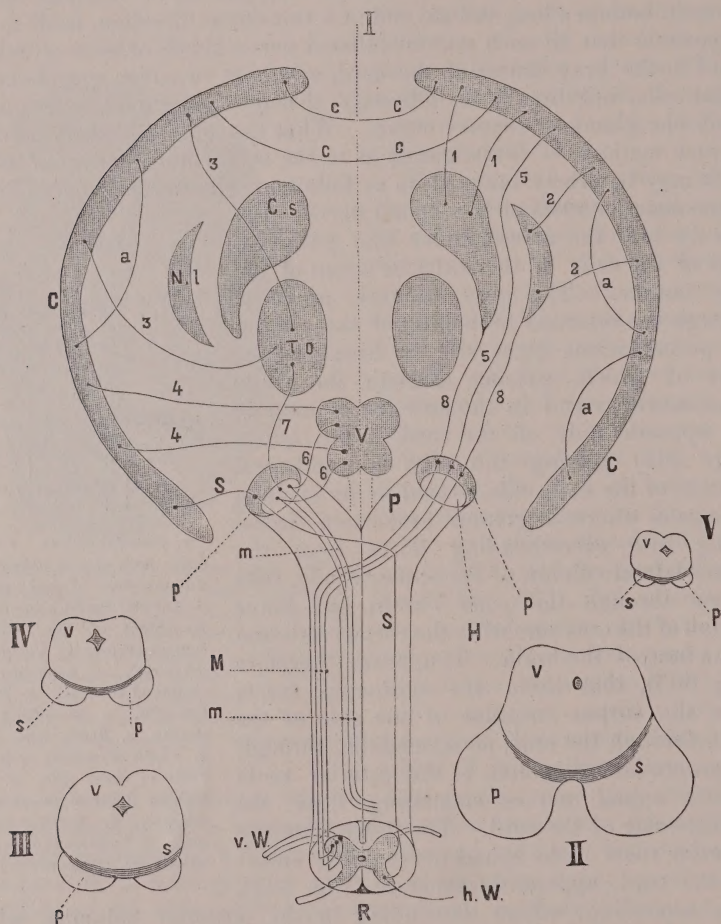


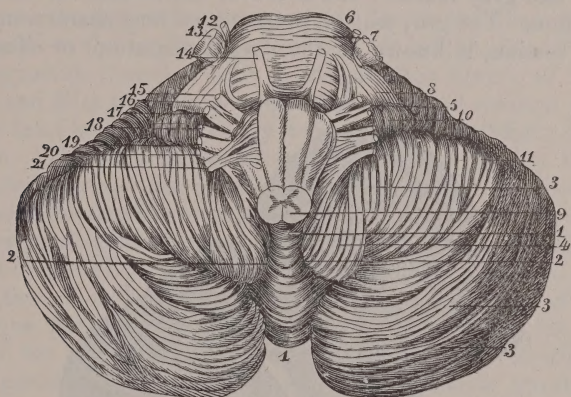
Diagram of the structure of the brain. C.C. Cortical substance of the cerebral hemispheres. C.S. Corpus striatum. N.l. Nucleus lenticularis. T.o. Thalamus opticus. V. Corpora quadrigemina. P. Pedunculus cerebri. P. Basis or crista, and II, tegmentum. 1, 1. Fibres of the corona radiata of the corpus striatum; 2, 2, those of the lenticular nucleus; 3, those of the optic thalamus; 4, 4, those of the corpora quadrigemina; 5, 5, direct strands to the cortex cerebri (Flechsig); 6, fibres from the corpora quadrigemina to the tegmentum; 7, fibres from the optic thalamus to the tegmentum; *m*, further course of these fibres. 8. Fibres from the corpus striatum and lenticular nucleus to the pes of the pedunculus cerebri; *M*, further course of these fibres. S.S. Course of the sensory fibres. R. Transverse section of the spinal cord; v.W., anterior roots; h.W., posterior roots of the spinal nerves; *a*, *a*, association fibres; *c*, *c*, commissural fibres. (CARPENTER)

thence by the lateral columns through the medulla, pons, and upper portions of the crus cerebri to the thalamus opticus at the base of the brain, it would appear that there are also continuous tracts (Figs. 363,

364) passing from the thalamus opticus on one side of the brain through the crus, pons, medulla, and gray matter of the same side to the posterior roots of the spinal nerves emanating from the opposite side of the cord. From what has just been said, it is obvious that, while for convenience' sake, the spinal cord may be described as beginning at the great foramen, as a matter of fact, it passes so continuously into the medulla that the latter may be regarded as its upper expanded portion, and, since the medulla is largely made up of fibres from the cords passing through it to the basal ganglia, corpora striata, thalami optici, etc., the cord, physiologically, may be regarded as beginning in these ganglia at the base of the brain, rather than at the great foramen.

The medulla oblongata (Fig. 364) is of a pyramidal form, having its broad extremity upward and expanded laterally at its upper part. Its

FIG. 364.



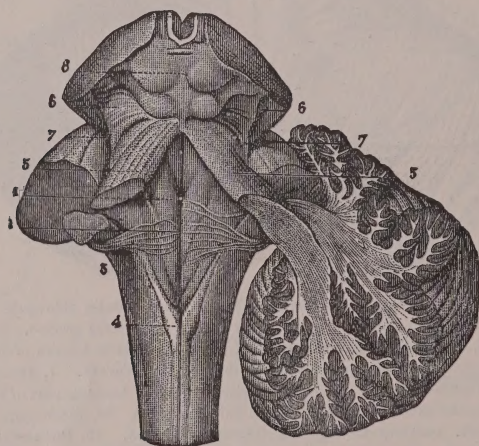
Inferior surface of the cerebellum with the pons Varolii and medulla oblongata. 1. Placed in the notch between the cerebellar hemispheres, is below the inferior vermiform process. 2, 2. Median depression, or vallecule. 3, 3, 3. The biventral, slender, and posterior inferior lobules of the hemisphere. 4. The amygdala. 5. Flocculus, or subpeduncular lobule. 6. Pons Varolii. 7. Its median groove. 8. Middle peduncle of the cerebellum. 9. Medulla oblongata. 10, 11. Anterior part of the great horizontal fissure. 12, 13. Smaller and greater roots of the fifth pair of nerves. 14. Sixth pair. 15. Facial nerve. 16. Pars intermedia. 17. Auditory nerve. 18. Glosso-pharyngeal. 19. Pneumogastric. 20. Spinal accessory. 21. Hypoglossal nerve. (From SAPPEY, after HIRSCHFELD and LEVEILLÉ.)

length is about an inch and a quarter, its breadth nearly an inch, and its thickness about three-quarters of an inch. Like the spinal cord, the medulla presents two median fissures. The anterior median fissure terminates just below the pons in a recess, the foramen cæcum of Vicq d'Azyr; the posterior is, however, continued up into the floor of the fourth ventricle, where, after expanding into a superficial furrow, it is gradually lost. In other respects, however, the medulla differs entirely in the arrangement of its parts from the spinal cord, each of its halves being characterized by four eminences, or columns, which are known in the order in which they present themselves from before backward as the anterior pyramids, the olivary bodies, the restiform bodies, and the posterior pyramids. The anterior pyramids are situated on either side of the anterior fissure, and are separated from the olivary bodies



by a slight depression. Each anterior pyramid consists of two sets of fibres, inner and outer: the outer fibres are continuations of those of the anterior columns of the cords of the same side, and, together with the decussating fibres from the opposite side of the cord pass upward through the pons into the cerebral peduncles; the inner or decussating fibres, so called because they interlace, to a considerable extent, with those of the opposite pyramid, are, in reality, almost entirely derived from the fibres of the lateral column of the opposite side of the cord, the anterior pyramids being pushed aside, as it were, by the lateral columns inserting themselves between them as they interlace with each other. The anterior pyramid proper contains no gray matter, its so-called nucleus consisting of stellate nerve cells lying behind and between it and the olivary body. The olivary bodies are two smooth oval eminences sunk deeply into the medulla, and consist of both white and gray matter; the fibres of the former run in a longitudinal direction. The gray matter, presenting a very characteristic zigzag contour in section, is known as the corpus dentatum, or ciliare, or oli-

FIG. 365.



View of the floor of the fourth ventricle with the posterior surface of the medulla oblongata and neighboring parts. On the left side the three cerebellar peduncles have been cut short; on the right side the white substance of the cerebellum has been preserved in connection with the superior and inferior peduncles, while the middle one has been cut short. 1. Median groove of the fourth ventricle with the fasciculi teretes, one on each side. 2. The same groove at the place where the white striæ of the auditory nerve emerge from it to cross the floor of the ventricle. 3. Inferior peduncle or restiform body. 4. Posterior pyramid; above this the calamus scriptorius. 5. Superior peduncle, or processus a cerebello and cerebri; on the right side the dissection shows the superior and inferior peduncles crossing each other as they pass into the white centre of the cerebellum. 6. Fillet to the side of the crura cerebri. 7. Lateral grooves of the crura cerebri. 8. Corpora quadrigemina. (From SAPPET after HIRSCHFELD and LEVEILLÉ.)

vary nucleus; while the gray lamina above the latter is often described as the accessory olivary nucleus. The fibres of the anterior columns of the cord, which, as just mentioned, are thrown outward as they are continued up as the outer fibres of the anterior pyramids, pass partly on the outside of, and partly beneath the olivary bodies, and being joined by fibres from the olivary nucleus pass upward as the olivary fasciculus

and fillet to the corpora quadrigemina and cerebral peduncles. The restiform bodies, or the inferior peduncles of the cerebellum, situated behind and to the outer side of the olivary bodies (Fig. 365), while containing a considerable quantity of gray matter, consist principally of white fibres continued upward partly from the posterior column of the cord, and partly from the lateral and anterior columns; the latter fibres, a small band, connect the anterior column with the cerebellum. The posterior pyramids situated on either side of the posterior median fissure, containing much gray matter, consist of white fibres, continuous with those of the posterior median columns of the cord; ascending, they diverge from one another, forming the lower boundary of the fourth ventricle, and tapering off become closely applied to the restiform bodies.

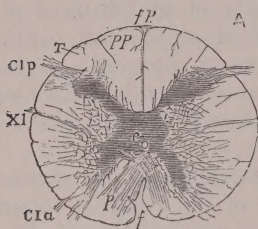
Resuming what has just been said with reference to the structure of the medulla, it will be seen that the fibres of the anterior columns of the cord pass through it by three routes: 1st, as the fibres of the anterior pyramids to the cerebral peduncles; 2d, as the inner fibres of the anterior pyramids (together with the decussating fibres), as the olivary fasciculus and fillet to the corpora quadrigemina and cerebral peduncles; 3d, as the band behind the olivary body, from the restiform body to the cerebellum. The fibres of the lateral columns pass through the medulla also by three routes: 1st, as the decussating fibres (together with the inner fibres of the anterior pyramids), as the olivary fasciculus and fillet to the corpora quadrigemina, and cerebral peduncles; 2d, by the restiform body to the cerebellum; 3d, by the fibres in the floor of the fourth ventricle (fasciculus teres) into the cerebrum. The fibres of the posterior columns pass through the medulla by two routes: 1st, the outer portions of the columns by the restiform bodies to the cerebellum; 2d, the inner portion (fasciculus gracilis), by the posterior pyramids to the cerebrum.

The fourth ventricle (Fig. 365), just alluded to incidentally, is the space left between the medulla oblongata in front, and the cerebellum behind. It is bounded laterally by the superior peduncles above, and by the diverging posterior pyramids and restiform bodies below, and is covered in behind by the valve of Vieussens and inferior vermiform process of the cerebellum, the floor being constituted by the back of the medulla oblongata and pons Varolii, marked by the median furrow terminating inferiorly as the calamus scriptorius; above the fourth ventricle communicates through the sylvian aqueduct or iter with the third ventricle, and below with the central canal of the spinal cord and the subarachnoid cavity through the foramen of Magendie in the pia mater. The gray matter of the floor of the fourth ventricle disposed as a continuous series of nuclei extending from beneath the corpora quadrigemina to a point corresponding to the decussation of the pyramids, is of extreme interest physiologically as constituting, as we shall see, the nuclei of origin of the so-called cranial nerves from the third to the twelfth inclusive. The gray matter of the medulla, like that of the spinal cord proper, differs as regards its form, amount, etc., according to the position of the section. Thus, if the latter be made just above the level of the first cervical nerve (Fig. 366), the central gray



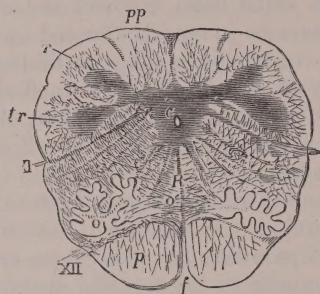
substance is encroached upon, pushed back by the decussating fibres from the lateral columns, which, in coursing inward, separate the anterior cornu from the rest of the gray substance, while if the section be made through the lowest part of the olivary bodies (Fig. 367), the

FIG. 366.



Transverse section of the medulla oblongata, showing the arrangement of the gray matter.

FIG. 367.



gray matter will be seen to be still further modified. The pons Varolii entering, as we have seen, into the formation of the floor of the fourth ventricle, consists not only of the longitudinal fibres passing upward through it from the cord and medulla to the crura cerebri, but also of commissural fibres connecting the lateral halves of the cerebellum and of gray matter. The functions of the latter will be considered after those of the spinal cord and medulla have been treated of.

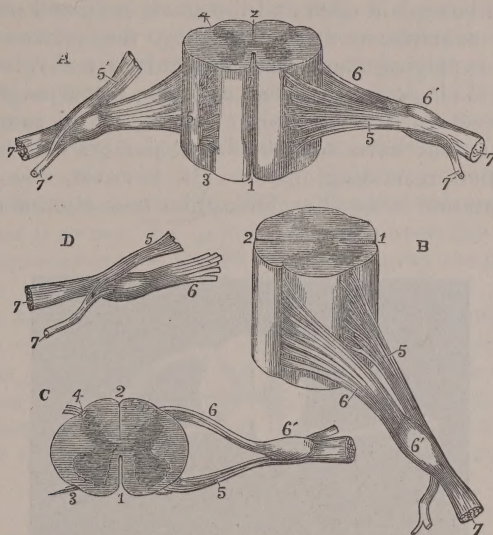
From the fact of the spinal nerves being distributed in general to the muscles of the trunk and extremities, the sphincters, and to the integument covering these parts, of the posterior part of the head, and a portion of the mucous membrane, it is evident that a complete account of their functions would necessitate not only a detailed description of each spinal nerve, but of the parts supplied by the latter. Inasmuch, however, as a knowledge of the properties of the spinal nerves in general will enable one usually to perceive from the anatomical relations involved in the functions of any one of them, a brief description of these nerves only will be given, the student being referred for details to the classical treatises on anatomy.<sup>1</sup>

There are thirty-one pairs of spinal nerves, eight cervical, twelve dorsal, five lumbar, five sacral, and one coccygeal. Each spinal nerve (Fig. 368, A B) arises from the cord by an anterior and a posterior root, the latter being the largest, and having a ganglion. Immediately beyond the ganglion the two roots unite into a single spinal nerve, which, after passing out of the spinal canal by the intervertebral foramen (with the exception of the sacral and coccygeal nerves, which divide within it), divides into two branches, anterior and posterior, distributed respectively to the anterior and posterior portions of the body, the anterior branch being the largest. It will be observed that a distinc-

<sup>1</sup> It may be mentioned in this connection, that the author is accustomed to illustrate his lectures on the spinal, as also the cerebral and sympathetic nerves, by means of the oxyhydrogen lantern and colored photographs of Hirschfeld's and Leveillé's plates. The latter, furnished for the author by Queen & Co., are models of artistic work, and give the student an excellent idea of the whole nervous system.

tion is made between the anterior and posterior roots of a spinal nerve and its anterior and posterior branches. The significance of this distinction will become at once apparent after it has been shown experi-

FIG. 368.



Different views of a portion of the spinal cord from the cervical region, with the roots of the nerves slightly enlarged. In A, the anterior surface of the specimen is shown, the anterior nerve-root of its right side being divided; in B, a view of the right side is given; in C the upper surface is shown; in D, the nerve-roots and ganglion are shown from below; 1, the anterior median fissure; 2, posterior median fissure; 3, anterior lateral depression, over which the anterior nerve-roots are seen to spread; 4, posterior lateral groove, into which the posterior roots are seen to sink; 5, anterior roots passing the ganglion; 5', in A, the anterior root divided; 6, the posterior roots, the fibres of which pass into the ganglion 6'; 7, the united or compound nerve; 7', the posterior primary branch, seen in A and D to be derived in part from the anterior and in part from the posterior root. (FROM QUAIN.)

mentally that the anterior root is purely motor in function, and the posterior root purely sensory, whereas the anterior branch, consisting of fibres derived from both the anterior and posterior roots, will be found to be both motor and sensory in function, and the posterior branch being made up also of fibres derived from both the anterior and posterior roots is also motor and sensory in function. The anterior and posterior branches of a spinal nerve are therefore mixed in their function, whereas the anterior root is purely motor, and the posterior root wholly sensory.

The discovery that the anterior root of a spinal nerve is motor, the posterior root sensory in function, is an excellent illustration of the indispensability of vivisection as a means of research in physiological investigation—indeed, it is difficult to conceive how the discovery could have been made in any other manner, comparative anatomy, from the nature of the case, throwing no light upon the question, since the spinal nerves arise in a similar manner in all vertebrates, while pathological changes, even when recorded from involving both roots simultaneously, rendered such data of little or no use. Such being the case,



the only available means of investigation was experimental, and, as a matter of fact, it was by such means, a vivisection, that Magendie<sup>1</sup> first demonstrated the function of the roots of the spinal nerves, one of the most important discoveries ever made in the whole range of science, which, on account of its importance, will now be repeated. The vertebral canal being laid open and the spinal cord and nerves exposed in a frog, for example, or a rabbit or dog, the anterior roots of the spinal nerves supplying the lower extremity are divided. Allowing sufficient time to elapse for the effect of shock, hemorrhage, etc., to pass off, it will be observed that the lower extremity on the same side as that on which the nerves have been divided is paralyzed so far as regards motion, sensation remaining intact. If, however, the distal end of the divided anterior roots (Fig. 369, *c*) be now stimulated, the lower

FIG. 369.

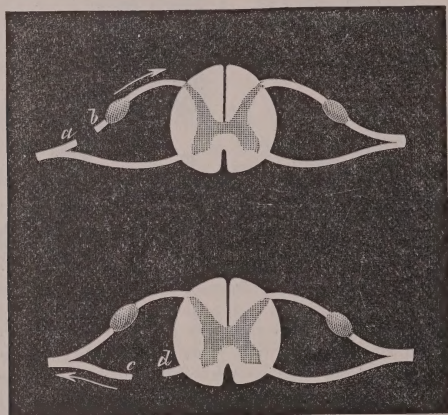


Diagram of spinal cord and nerves. The posterior root is seen divided at *a*, *b*, the anterior at *c*, *d*.

extremity will be at once thrown into muscular contraction, whereas no effect is observed, on the other hand, either of a motor or sensory character, if the central end *d* of the divided anterior root be stimulated. These facts show conclusively that the functions of the anterior roots of the spinal nerves is motor, and that the stimulus emanating from the cord, whatever its nature may be, is transmitted through the anterior root from the centre to the periphery. That the anterior root possesses in itself no sensory properties is shown from the fact that even if at times signs of sensibility manifest themselves on its stimulation, such sensibility at once disappears after division of the posterior root, the sensibility occasionally exhibited on stimulation of the anterior root being due either to muscular cramp produced, as suggested by Brown-Séquard,<sup>2</sup> or to there being recurring fibres passing backward from the anterior root through the posterior root to the cord, hence the name of recurrent sensibility given to the phenomenon by Magendie<sup>3</sup> and Longet.<sup>4</sup>

<sup>1</sup> Journal de physiologie, tome ii. pp. 276, 368. Paris, 1822.

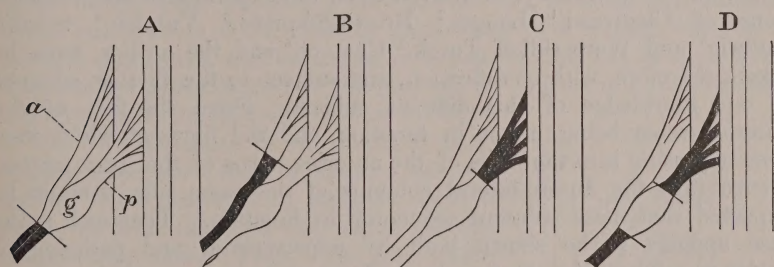
<sup>2</sup> Physiology and Pathology of the Central Nervous System, p. 8. Philadelphia, 1860.

<sup>3</sup> Comptes Rendus, t. xxiv. p. 3. Paris, 1847.

<sup>4</sup> Bernard : Systeme Nerveux, tome i. p. 35. Paris, 1858. Physiologie, tome iii. p. 115. Paris, 1869.

If, now, the posterior roots of the spinal nerves in the same animal, but on the uninjured side, be divided, it will be observed that while the animal retains the power of moving the lower extremity it has lost sensation entirely in it, and that while no effect is observable if the distal end (*a*, Fig. 369) of the divided posterior root be stimulated, sensibility at once manifests itself if the central end (*b*) of the same be stimulated, showing conclusively that the function of the posterior root of the spinal nerve is sensory, and that the impression made upon the periphery is transmitted through the posterior root to the cord. That the posterior root possesses in itself no motor properties is shown from the fact that if the anterior root be divided no motion ever ensues on stimulating its central end, any motion ensuing on stimulation of the central end of the posterior root being reflex in character, a kind of recurrent motility, so to speak—that is to say, the impression made upon the central end of the divided posterior root is transmitted to the gray matter of the cord, and is thence reflected out through the anterior root. While the ganglion already mentioned, so characteristic of the posterior roots of the spinal nerves, does not appear to influence in any way the transmission of impressions from the periphery to the centres, it does exercise a very great influence upon the nutrition of the nerves after their division. Thus it has been shown by Waller,<sup>1</sup> if the roots be divided between the ganglion and the cord (Fig. 370), that while the central end of the

FIG. 370.



Degeneration of spinal nerves and nerve roots after section. A Section of nerve trunk beyond the ganglion. B. Section of anterior root. C. Section of posterior root. D. Excision of ganglion. *a*. Anterior root. *p*. Posterior root. *g*. Ganglion.

anterior root preserves its normal structure, the distal end degenerates, exhibiting the usual changes undergone by a nerve when separated from its centre; whereas, in the case of the posterior root it is the distal end, that attached to the ganglion, which remains normal, the central end degenerating. It would appear, therefore, from these experiments, that the ganglion of the posterior roots exerts a nutritive influence upon the sensitive nerves, like that exerted by the spinal or higher centres on motor ones, and it is worthy of observation that the degeneration takes place in the direction in which the nerve force is transmitted. In this connection it may be mentioned also, as confirmatory of the explanation offered of recurrent sensibility, that if the posterior root be divided

<sup>1</sup> Comptes Rendus, tome xlv. p. 168. Paris, 1857.



beyond the anterior roots will then be found to contain degenerated fibres, showing that some of the fibres of the anterior root at least are really derived from the posterior one. While there can be no doubt that the spinal cord is the exclusive organ of communication between the brain on the one hand, and the external organs of sensation and motion on the other, a complete loss of sensibility and voluntary motion following its division, compression, or disorganization; there still prevails some uncertainty as to the exact routes by which impressions made upon the periphery are transmitted from the posterior roots through the cord to the sensorium and voluntary impulses in the reverse direction through the anterior roots to motor organs.

The difference of opinion held in this respect by physiologists, the diametrically opposed views that have been maintained, are no doubt due partly to the fact of the structure of the spinal cord not yet being thoroughly understood either in man or animals, pathological facts, therefore, being of little use as a means of discovering its functions, but also in a great measure to the conclusion based upon experiments performed upon animals being applied to man without it being taken into consideration that not only does the spinal cord of animals differ in certain respects from that of man, but that it varies in its structure in different parts of its course even in the same animal. The brief expose that we have to offer of the functions of the spinal cord in man as a conductor of sensory and motor impulses to and from the periphery, as derived from the experiments and observations of Chauveau,<sup>1</sup> Longet,<sup>2</sup> Brown-Séquard,<sup>3</sup> Vulpian,<sup>4</sup> Schiff,<sup>5</sup> Ludwig<sup>6</sup> and Woroschiloff Turck,<sup>7</sup> Charcot,<sup>8</sup> and the author, must be taken, therefore, with qualification, and subject to the further advance of our knowledge of this difficult subject. From the fact of the anterior roots being motor in function, and the fibres of which they consist passing into the cells of the anterior horns of the gray matter, thence into the antero-lateral columns of the same side, it might be expected that these columns are motor in function. That such is the case appears to be shown both by experimental and pathological evidence. Thus, if a section be made in an animal, a rabbit, guinea-pig, or dog, for example,<sup>9</sup> involving only the antero-lateral columns of one side of the cord there is entire loss of the power of voluntary motion on that side below the level of the section, while if the columns be stimulated at their distal ends, the muscles supplied by the portion of the cord below the section will be thrown into contraction. On the other hand, if the posterior columns and the gray matter of the cord be divided, the antero-lateral columns, however, being uninjured, the power of voluntary motion is preserved, that of sensibility and muscular

<sup>1</sup> Journal de la Physiologie, tome iv. p. 369. Paris, 1861.

<sup>2</sup> Anatomie et physiologie du système nerveux, tome i. p. 272. Paris, 1842. And Physiologie, tome iii. p. 338. Paris, 1869.

<sup>3</sup> Physiology and Pathology of the Central Nervous System. Philadelphia, 1860.

<sup>4</sup> Leçons sur la physiologie générale et comparée du système nerveux. Paris, 1866.

<sup>5</sup> Lehrbuch der Physiologie.

<sup>6</sup> Verhandlungen der Königlich Sachsischen Gesellschaften zu Leipzig, 1875, iii. iv. v. S. 248.

<sup>7</sup> Wiener Denkschriften, 1851.

<sup>8</sup> Leçons sur les Localisations dans les maladies du cerveau et de la moelle épinière. Paris, 1880.

<sup>9</sup> In making sections of the cord in an animal it is indispensable that the spinal column should be firmly fixed, and that the cord be denuded within certain defined measurable areas. These conditions are fulfilled by using the instrument devised by Ludwig and Woroschiloff, and described in Ludwig's Arbeiten, 1875.

coördination is lost. The available pathological evidence confirms also what has been learned from histological examination of the cord of man and experiment upon animals, that of the motor fibres in the antero-lateral columns, and more especially in the lateral ones, by far the most of them pass down continuously from the corpus striatum of one side of the base of the brain through the crus, pons, medulla, thence to the opposite side of the cord, and down the lateral columns, connecting in them with the prolongations of the cells in the anterior horns of the gray matter, which in turn are connected with the fibres of the anterior roots. Thus, disorganization beginning in the corpus striatum or thereabouts, progresses gradually downward through the tract just mentioned, involving motor paralysis.

In the study of the functions of the corpus striatum more especially, additional facts will be mentioned, confirming the view just advanced that the antero-lateral columns of the cord, more particularly the lateral portions, are motor in function, and are the routes by which motor impulses are transmitted from the base of the brain to the periphery. That the gray matter of the cord is essentially that portion of it which transmits the impressions made upon the periphery to the sensorium is shown by the fact of sensibility remaining as long as the gray matter preserves its normal structure, even after all the columns have been divided, and by the experiment just mentioned, in which sensation is lost after division of the gray matter, and the posterior columns, the latter owing what sensibility they possess not to their own intrinsic fibres, but to those of the posterior roots which pass through them in an upward, downward, and horizontal direction, on the way to their termination in the posterior horn of the gray matter. Now it is an interesting and important fact that while the motor fibres of the cord decussate in the medulla, pathological cases show that in man at least the sensory fibres decussate in the cord itself, at about the level in which they enter through the posterior roots. Thus, if the gray matter of the cord and lateral column be divided in man on one side, as by the penetration of some sharp instrument, or compressed by a tumor or disorganized by disease, as in cases that have come under the observation of the author and others, sensibility is lost on the side of the body below, but opposite to the side on which the wound has been inflicted, or the tumor located, the power of voluntary motion, however, being lost on the same side of the body as that of the wound, etc.

(Fig. 371, 3). If the section be made, however, at a higher level as at 2 or 1, then the paralysis of both motion and sensation will be on the same side of the body, but on the opposite side to that of the section. It follows, also, that if the spinal cord be divided longitudinally below the medulla, in a dog, for example, that while the animal is able to stand on his four legs and make voluntary movements, as first shown

FIG. 371.

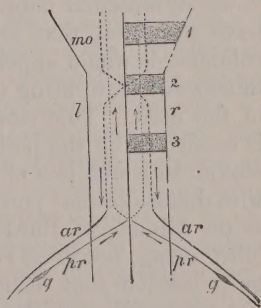


Diagram showing the course of the motor and sensory fibres in the spinal cord and medulla oblongata.



by Galen,<sup>1</sup> it has lost all sensibility in them, all the sensory fibres being divided at their decussation in the middle line, the motor fibres remaining uninjured by the section.

While there can be but little doubt that the decussation of the sensory fibres in the spinal cord of man is complete, such does not obtain, to the same extent, in all animals, the decussation being much less complete in reptiles and birds than in mammals, and less in the lumbar than in the dorsal portions of the cord in certain animals. In connection with the anæsthesia of the opposite side of the body following a hemisection of the cord may be here appropriately mentioned the hyperæsthesia usually developed in the same side as that of the section. This remarkable condition of excited sensibility, made quite evident within a few hours after the operation by the movements of the animal made in response to the slightest pinching, etc., of the skin, and lasting often for weeks, is probably due to the increase in temperature and vascularity brought about by the division of the vasomotor nerves, or the nerves regulating the calibre of the bloodvessels, which, we shall see hereafter, descending from the vasomotor centre in the medulla oblongata through the antero-lateral columns, but is also, no doubt, to be attributed to the division of the inhibitory or restricting fibres, whose influence being lost, therefore, upon the parts below the section, the latter becomes more excitable, more susceptible to external stimulus.

It is a remarkable fact that, while the gray matter of the cord transmits sensory impressions, it itself appears to be insensible to ordinary mechanical or electrical stimuli, since it may be pricked, pinched, or electrically stimulated without the animal giving any signs of pain. The gray matter can be, however, excited by chemical stimuli, certain poisons, and venous blood. It has already been mentioned that if the posterior columns and the gray matter of the cord are divided, that the power of muscular coördination, as well as sensibility is lost, and, as we have just seen, that sensibility cannot be attributed to the posterior columns, it would appear that the function of the posterior columns is to coördinate, to bring together in harmonious action, different portions of the cord. This view, based upon experiments made upon animals, is confirmed by the pathological evidence afforded by cases of locomotor ataxia, in which loss of the power of muscular coördination is associated with disease of that portion of the posterior columns of the cord known as the columns of Burdach, the power of voluntary motion and sensibility being, however, retained. It may be here mentioned that it is quite possible that such portions of the anterior columns not containing the motor fibres of the anterior roots, like the posterior columns, may be also commissural, coördinating in character. It must be mentioned in this connection, with what has been said as to the result of division of different parts of the spinal cord, that from the fact of the loss of the power of voluntary motion and sensibility being frequently restored, that there must exist potentially, so to speak, a vicarious power of interchange of function between different parts of the cord, certain fibres

<sup>1</sup> De Anat. Administrat. Lib. viii. Cap. v., Opera Omnia, t. ii. p. 683. Lips., 1821.

Galen does not appear, however, to have observed the loss of sensibility in such cases, which was first observed by Fedora in 1822, *Journal de Physiologie*, t. iii. p. 199. Paris, 1823.

being capable, if necessary, of assuming the power of transmitting sensory and motor impulses, in addition to their ordinary characteristic functions.

Resuming, it may be said, in all probability, that in man, at least, usually the fibres conducting motor impulses pass from the corpus striatum from one side of the brain down through the lateral column, principally of the opposite side of the cord through to the gray matter to the anterior roots, that the fibres transmitting sensory impressions pass from the posterior roots to the gray matter of the opposite side of the cord upward in the gray matter to probably the thalamus opticus, and that the function of the anterior and posterior columns is commissural, coördinating in character. Finally, if it be admitted that there is no essential difference between motor and sensory nerves, then the anterior root of the spinal nerves is motor, because the fibres of which it consists terminate in muscle, and the posterior sensory, because its fibres begin in sensory organs. Having demonstrated now experimentally this important distinction in function between the roots and the branches of the spinal nerves, and offered an explanation of the cause of the same, let me briefly point out the general distribution of the anterior and posterior branches, it being always borne in mind that the branches, whether anterior or posterior, are in their functions mixed nerves, possessing both motor and sensory properties. The anterior branches of the four upper cervical nerves form the cervical plexus, and the four lower cervical, together with the first dorsal nerve, the brachial plexus. From the cervical plexus are derived the superficial cervical, great auricular, small occipital, supraclavicular, and phrenic nerves, and muscular branches; the brachial plexus supplying mainly the upper extremity, but giving off, also, the supra- and subscapular and thoracic nerves. The posterior branches of the cervical nerves, with the exception of the first, after passing backward from the vertebral canal divide into external and internal branches, and supply the muscles and integument behind the spinal column, the posterior branch of the first cervical issuing between the arch of the atlas and the vertebral artery, being distributed to the contiguous straight, oblique, and complex muscles.

The anterior branches of the dorsal or thoracic nerves, with the exception of the last one, pass outwardly in the intercostal spaces, as the intercostal nerves, the anterior branch of the last dorsal being situated below the last rib crosses the quadratus lumbæ muscle as it advances between the internal oblique and transverse muscle in a similar manner as an intercostal nerve. In their course the intercostal nerves, as they supply the muscles, give off lateral cutaneous branches, that from the second intercostal or the intercosto-humeral nerve being an important one, since it extends across the axillary space, running in juxtaposition with the small cutaneous nerve from the brachial plexus, and supplies the skin on the inner part of the arm. The posterior branches of the dorsal nerves, like those of the spinal nerves, generally, after turning backward between the transverse processes of the vertebræ, divide into external and internal branches, the former supplying the skin contiguous to the angle of the ribs, the longissimus and sacro-lumbæ muscles, the latter the skin over the spinous processes of the



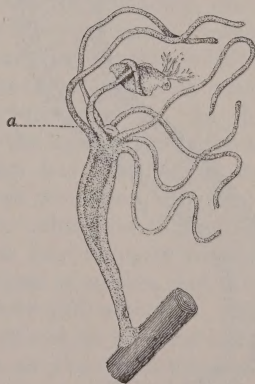
vertebræ, the multifid and semispinal muscles. The anterior branches of the upper four lumbar nerves, together with a filament from the last dorsal nerve, constitute the lumbar plexus, and which, after supplying the psoas and quadratus lumbar muscles, give off the ilio-hypogastric, ilio-inguinal, genito-crural, external cutaneous, obturator and anterior crural nerves. The posterior branches of the lumbar nerves pass backward, like those of the dorsal, to supply the longissimus and sacrolumbar muscles, and the adjacent skin. The anterior branches of the upper four sacral nerves, together with the fifth and part of the fourth lumbar nerves, form the sacral plexus, from which are derived the filaments supplying the pyriform, internal obturator muscles, etc., the levator and sphincter ani, the superior gluteal, pudic, and great and small sciatic nerves. The sacral, together with the lumbar plexus, give off the nerves supplying the lower extremity. The anterior branch of the fifth sacral, a small nerve, emerges from the end of the vertebral canal, and divides into two branches, one of which passes with a filament from the fourth sacral to end in the sympathetic, the other joining the coccygeal nerve. While the posterior branches of the upper four sacral nerves pass out of the vertebral canal by the corresponding sacral foramina, the posterior branch of the fifth sacral emerges from the end of the vertebral canal, and, together with the posterior branch of the coccygeal nerve, supplies the skin and muscles of the back. The anterior branch of the coccygeal nerve also passes out of the end of the vertebral canal, is joined by a branch from the fifth sacral after perforating the coccygeal muscle and great sacro-sciatic ligament, and terminates in the skin of the buttock. The posterior branch of the coccygeal, like the anterior branch, emerges from the end of the vertebral canal; its distribution has just been referred to in connection with that of the posterior branch of the fifth sacral.

## CHAPTER XLI.

### THE SPINAL CORD AS A NERVOUS CENTRE. REFLEX ACTION.

ONE of the most striking differences in the organization of animals is the extent to which the division of labor, physiologically speaking, is carried. Indeed, the lowest forms of life, such as the monera (consisting, as we have seen, of mere masses of protoplasm), are so utterly unorganized as to make it impossible to say whether such things should be assigned genealogically to the vegetable or animal kingdom. It is true, that among such primitive forms of life there are beings, like the common amœba, in which there is a slight differentiation of structure, in that not only a nucleus and nucleolus are present, but that, at times, even an enveloping membrane or cell wall is developed, and that among the infusoria are also seen forms, like paramœcium, apparently quite organized; nevertheless, even these protozoan animalculæ, so much more complex in their structure than the monera, cannot be said to be organized in the same sense that the remaining members of the animal kingdom, or metazoa are. Even the infusoria, apparently complex as they are in their structure, are morphologically only unicellular, and never passing beyond this primitive one-celled stage; tissues, and still less organs, are never developed in them similar to those of which the body of one of the higher animals is made up, since, as we have already seen, the organs in the latter consist of tissues and the tissues of cells, the latter resulting from the division of the primitive cell. Indeed, it is not until we reach in the tree of life the porifera, actinozoa, and hydrozoa, of which the sponge, anemone, and jelly fish, familiar objects at the sea-shore, are examples, that we meet with anything like organization, at least in the true morphological sense of the word—that is to say, of an animal consisting of organs made up of tissues developed out of cells resulting from the segmentation of a primitive cell, or ovum. Suppose that the structure of one of the hydrozoa be considered as that of the common green hydra (Fig. 372), found during the summer in almost every fresh water pool, and therefore an object for study accessible to all, it will be found that the animal, about half an inch in length and a line in diameter, is essentially a double-layered tube, closed at one end and open at the other, the latter serving as a mouth and surrounded with slight tentacles, or feelers, by means of which it seizes its

FIG. 372.



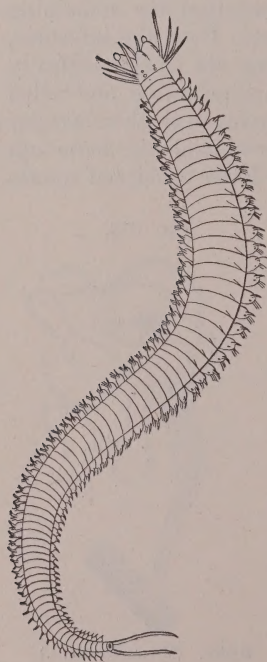
Hydra. (MILNE EDWARDS.)



prey, the outer layer, or ectoderm, of the tube, functioning as skin, the inner layer, or endoderm, as a mucous digestive surface.

Leaving out of consideration an imperfectly developed neuromuscular layer or mesoderm intermediate between the ectoderm and endoderm (absent in the protohydra), the hydra may be considered functionally as little more than a digestive sac. That the differentiation of ectoderm and endoderm is very incomplete, is shown from the fact that if the animal be turned inside out the skin or ectoderm becomes digestive in function, and the digestive surface or endoderm epidermal, just as the mucous membrane of the mouth or anus in man may become skin if everted, or the skin of the same parts mucous membrane if inverted. This is, however, as might have been expected, since, as we shall see hereafter, there can be little doubt but that the ectoderm and endoderm of the hydra are homologous with the epiblast and hypoblast of the embryo, or the parts corresponding to the skin and mucous membrane of the adult. Further, that no one part of the hydra differs essentially from any other part, is shown by the well-established fact that if a hydra be cut up into several pieces each piece will live and lead an independent existence and develop into a perfect hydra. While, at first sight, such a result may appear as a

FIG. 373.



very extraordinary one, it becomes a perfectly natural and intelligible one when it is remembered that all parts of the body of the hydra have essentially the same function, and that there is no interdependence between the parts of which it consists. Reproduction by fission, whether produced artificially or naturally, is not confined, however, by any means to such low forms of life as the hydra, being observed as well in quite highly organized animals as among the annelida, of which the marine worms, such as the clam worm (*Nereis pelagica*) of our coasts (Fig. 373), etc., are examples. The body of a nereid worm, consisting of numerous segments, is naturally very apt to break up into numerous pieces consisting of one or more of the segments, as the animal glides along among the rocks, sand, or sea-weed, each piece becoming, under favorable circumstances, a perfect animal. Indeed, at certain seasons of the year there may be seen in certain kinds of these worms (protura) at different portions of the body constrictions indicating the parts where the body will break up, by natural fission, into a progeny of worms. That such a mode of reproduction should take place in an animal as highly organized as those just mentioned, having a distinct body cavity inclosing a nervous system, ali-

mentary canal, heart, may appear even more extraordinary than the case of the hydra just referred to. It must be borne in mind, however,

that in the worm, as in the hydra, there is but little interdependence of parts, each segment having its own nervous ganglion and fractional part, so to speak, of the alimentary canal and vascular tubes running from end to end of the animal. In fact, an annelid may be regarded, morphologically, as consisting of a chain of small annelids (the segments depending but little upon each other, linked together, as it were, for only the time being). A glance now at the organization of a vertebrate animal, or even one of the higher invertebrates, will at once show how profoundly such an animal differs from any of those hitherto mentioned. The brain, as in man, for example, situated in the skull, depending for its activity upon the blood driven to it by the heart, in the thoracic cavity, the rhythmical action of the heart and lungs maintained by nervous influences emanating from the base of the brain, the alimentary canal within the abdominal cavity supplying the materials for the nourishment of the brain and other organs, but dependent upon the blood supplied to it by the heart for the elaboration of the alimentary secretions, illustrating sufficiently how intimate is the connection existing between the cranial, thoracic, and abdominal organs, and the impossibility of any one segment of the body containing such, living a life entirely independent of the remaining ones, as we have just seen is the case in many of the lower animals. This contrast between the lower and higher animals with reference to the extent with which the division of labor is carried on, is well illustrated by the difference between the savage and civilized state of society—and, indeed, the difference is something more than a mere comparison, being of a profound meaning to those who believe that the life of a nation is developed according to law as certainly as that of the individuals of which it is composed.

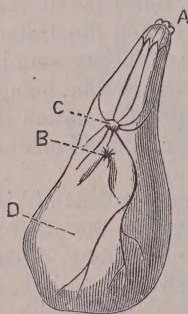
In the uncivilized, savage state, each individual is independent of his neighbors as the one segment of the worm may be to that of the other; his interest not being usually their interest—on the contrary, often antagonistic—he builds his simple hut, hunts his own game, clothes himself; a birth among his tribe adds to, a death takes away nothing from his daily life. Under such circumstances there can be no accumulation of wealth and the development incidental to it. In the civilized state, on the contrary, the interest of the one is the interest of all, as that of the one organ in the human body is that of the others; each individual confining himself to one avocation, the latter is advanced to its utmost limits, depending upon others for that which he does not produce himself, the product of his own industry reaches the highest perfection; and so with the productions of others, and thus the wealth of the nation increases both in variety and amount. Just as with the uncivilized, as compared with the civilized, so with the lower animals as compared with the higher ones; just as the development of a nation depends, not only upon the variety of the interests, but upon the mutual interdependence of the same; so the life of an animal is high in proportion to the variety of its organs, and the mutual harmonious working of the same. The famous example of the number of persons engaged in the making of nails or pins, and the great number



that can, consequently, be so produced, as mentioned by Adam Smith,<sup>1</sup> is as applicable as illustrating biological as well as politico-economical laws. The life of a man biologically as well as socially, when compared with that of a sponge, may be summed up in saying that in the former the division of labor is carried, so far as we yet know, to its utmost limits; in the latter but little, if at all. This division of labor, so characteristic of the higher animals, and which we have illustrated on account of its importance somewhat in detail, is not only well seen in the general organization of the higher animals, but in the extreme differentiation exhibited in their alimentary, vascular, nervous systems, etc., and as it is the functions of the latter that we are now more particularly considering, it will be well to illustrate the general structure of the nervous system in animals by a few examples before taking up the consideration of the subject of the reflex action of the spinal cord of man, the nature of which it is hoped will be made clearer by the preceding introductory than it would have been without it.

Of the simplest form of nervous system may be mentioned that of the ascidiordia, as seen, for example, in a phalusia, in which the entire nervous system consists (Fig. 374) of a single ganglion, receiving or

FIG. 374.



Nervous system of an ascidian. A. the mouth. B. The vent. C. The ganglion. D. The muscular sac.

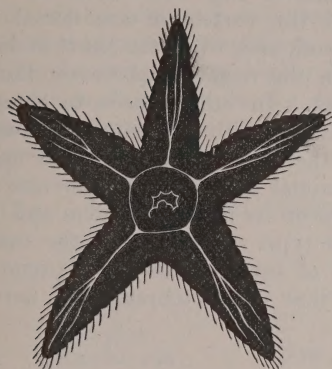
giving off filaments from or to the periphery. On touching this worm-like animal, and seeing it contract its body, judging from one's own feelings and actions, we would infer that the animal felt the touch, and voluntarily retracted its body, and conclude that the impression made upon the integument was transmitted by an afferent centripetal, or sensory nerve, to the ganglion, and there felt, and that the impulse emanating from the latter was transmitted by an efferent, or centrifugal, or motor nerve to the muscle, and there resulted in voluntary motion, the whole action being called a reflex one from the fact of the impression made upon the periphery being first transmitted to the ganglion and thence reflected back again. If the ganglion be not endowed with sensation and volition, then the animal must be without either, since it possesses no other structure of which such qualities can be predicated. Further, if muscular action, in response to stimuli applied to the periphery, is no evidence of either sensation or volition, then it is impossible to say whether any animal feels, or wills, under any circumstances. If now the nervous system of a starfish be compared with that of the ascidian, just mentioned, the only essential difference presented by the former is that, instead of one ganglion there are five (Fig. 375), which, together with the commissural filaments, constitute a circum-oral ring, from which are given off the nervous filaments supplying the rays.

It follows, therefore, that if the ganglion of the ascidian be endowed with sensation and volition, then all five ganglia of the starfish are

<sup>1</sup> An Inquiry into the Nature and Causes of the Wealth of Nations, vol. i. p. 7. Edinburgh, 1814.

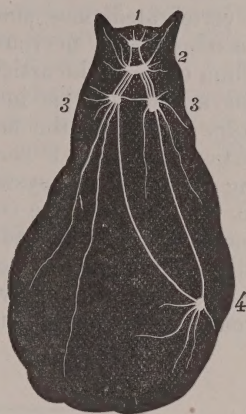
endowed with the same functions, the only difference between the two being that, in the one, whatever sensation and volition the animal may

FIG. 375.



Nervous system of starfish. (DALTON.)

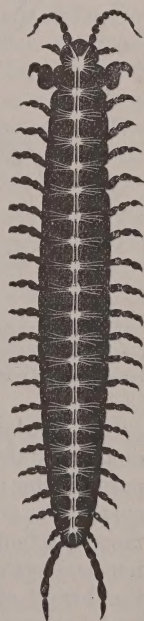
FIG. 376.



Nervous system of aplysia. (DALTON.)

be possessed of is concentrated in the single ganglion, whereas, in the other, the sensation and volition are diffused among the five ganglia. It is obvious, also, that, on account of the radial symmetry presented by the starfish, it is impossible to assign any special function to any one of the ganglia that is not possessed by the others. And, while even in the mollusca, of which the aplysia (Fig. 376), or sea hare, is an example, the supra-oesophageal ganglion (1) is regarded, morphologically, as a brain, there is little reason to suppose that it possesses, exclusively, any very specialized function not shared by the infra-oesophageal (2) one, or that the latter, in turn, differs very much, functionally, from the remaining ganglia (3, 4) distributed through the body, and with which it is connected by commissural filaments as well as with the supra-oesophageal one. It is true also, that the supra-oesophageal ganglion (Fig. 377) of centipedes, insects, etc., is usually spoken of as the brain of such animals, and the ventral chain of ganglia compared to the spinal cord of vertebrates, but, as some of the nerves in insects, for example, supplying the head, are derived from the supra-oesophageal ganglion, and others from the infra-oesophageal ganglion and, as the latter ganglion does not differ essentially from the remaining ones of which the ventral chain consists, it is difficult to see why any one ganglion should be designated as cerebral and the other as spinal. That there is no such essential difference between the so-called cerebral and spinal ganglion is shown from the fact that, if a worm breaks up into two,

FIG. 377.

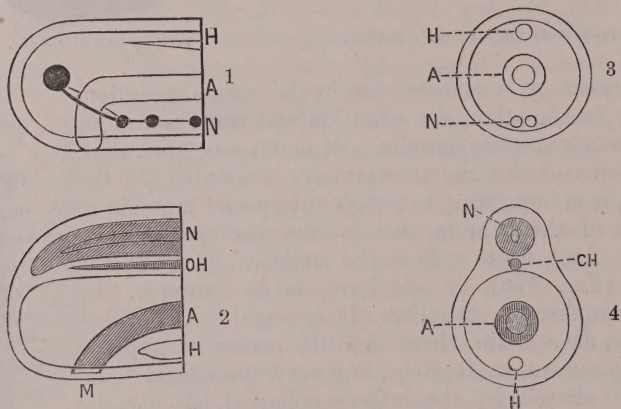


Nervous system of centipede. (DALTON.)



through fission, the ganglion that was central in the parent animal becomes anterior in the new individual, and goes to form its brain. Further, in the case of worms, insects, etc., it is questionable whether such animals are comparable at all as regards their nervous systems with vertebrated ones, since, as a glance at Fig. 378 will show, while the cerebro-spinal nervous centres of the vertebrate are dorsal, the ganglion chain of the articulate is ventral, and, while the heart is dorsal in the articulate, it is intermediate in the vertebrate between the alimentary canal and the nervous centre. In other words, to compare an articulated with a vertebrated animal, with reference to homologizing their nervous systems, one or the other must be placed upside down, and, however the vertebrated animal be placed, it is obvious that no comparison can be made at all between its nervous system and that of the echinodermatous or molluscus type. Such being the case, it would be illogical to apply the results of investigation made upon the nervous system of invertebrates to that of vertebrates, the nervous

FIG. 378.



Diagrammatic sections of an articulated invertebrate and vertebrate. 1. Longitudinal section of invertebrate. 2. Longitudinal section of vertebrate. 3. Transverse section of invertebrate. 4. Transverse section of vertebrate. H. Heart. A. Alimentary canal. N. Nervous system. CH. Chorda dorsalis.

system not being comparable in the two great divisions of the animal kingdom. For this reason, any conclusion as to the functions of the different parts of the nervous system in man, drawn from the study of the nervous system in animals, must be based upon that of the vertebrates only, more particularly of such classes in which the parts composing the nervous system can, without doubt, be homologized. The amphioxus, the lowest of vertebrates, being headless, offers, in the structure of its nervous system, absolutely nothing comparable with the brain of the remaining vertebrates. Unless it be denied that the amphioxus can feel or will, of which there is not the slightest evidence, it necessarily follows that the spinal cord of this primitive vertebrate, at least, is endowed with sensation and volition. If such be admitted, and it is difficult to see how the conclusion can be avoided, analogy would lead us to suppose

that the spinal cord of the lamprey and myxine, to a certain extent, at least, would possess, also, similar qualities, particularly as the sensation and volition exhibited by such animals are out of all proportion to the amount of brain present. Inasmuch, however, as these marsipobranchial fishes have a brain, or, at least, the basal ganglia of the brain of the higher vertebrates, it is to be inferred that, with these additional important structures, even if little developed, there would be exhibited corresponding higher faculties than shown by the amphioxus, and such is found to be the case, and, as we pass from these lowly organized vertebrates through the higher ones, to man, it will be observed, as may be seen from

TABLE LXXIII.—RATIO OF BRAIN TO SPINAL CORD.

|                     |       |      |
|---------------------|-------|------|
| Man . . . . .       | 33.0  | to 1 |
| Mouse . . . . .     | 4.0   | to 1 |
| Pigeon . . . . .    | 3.3   | to 1 |
| Triton . . . . .    | 0.550 | to 1 |
| Lamprey . . . . .   | 0.001 | to 1 |
| Amphioxus . . . . . | 0.0   | to 1 |

that the brain becomes more and more developed both relatively and absolutely with reference to the spinal cord, the extremes of the series being represented by man and the amphioxus respectively.

Now, as we have seen in general that the higher animals differ from the lower ones in the extent to which the division of labor is carried, the higher grade of life exhibited by the former depending upon the greater differentiation of their organization, the development of the brain just alluded to might have been anticipated, it being obviously of advantage that certain functions of the nervous system would be restricted to the brain, others to the spinal cord, and hence, as we shall see presently, the great development of the intellectual powers in the higher animals as compared with the lower ones. Further, it will be found that corresponding with this idea of the division of labor, that while the spinal cord of the lower vertebrates may possess both sensation and volition, that of the higher ones in becoming to a considerable extent a conductor of sensory and motor impulses loses such qualities, the seat of the sensorium and will being transferred to a higher plane, being gradually elevated, so to speak, in the higher animals. Thus while sensation and volition are diffused through the spinal nervous axis of the lowest vertebrates it gradually, through the process of development, becomes concentrated in the cranial expansion of that of the higher ones. The theoretical considerations just offered are fully borne out by experiment as well as by the facts of comparative anatomy. Thus, if a frog be decapitated and a drop of acetic acid be placed upon the skin near the anus<sup>1</sup> the animal keeps changing its position, and will endeavor to wipe off the acid by means of the foot of the same side of the body to which the acid was applied, and, if the latter be amputated, by means of the opposite foot. Not infrequently, also, the author has seen the animal try to remove the acid by one of the upper extremities, both legs having

<sup>1</sup> Pfäuger : Die Sensorischen Funktionen des Rückenmarks, 1853



been amputated. Considerable difference of opinion still exists as to whether such an action as that exhibited by a decapitated frog involves sensation and volition, or is to be regarded as a simple reflex action—that is, of an action such that an impression being made upon the skin of an animal and being transmitted by an afferent nerve to the gray matter of the cord, is thence reflected by an efferent nerve to a muscle without the animal necessarily feeling anything or making any voluntary effort. It appears to us, however, that a frog with its head on when stimulated by acetic acid gives but little more evidence of sensation and volition than with its head off when so stimulated, the difference exhibited between the cases being rather one of degree than of kind. Of course, the frog with its head on feels and wills more than with its head off, but it does not follow, in the latter case, that the animal does not feel or will at all. Indeed, if it be denied that the decapitated frog feels and wills, it becomes very questionable whether there is any way at all of positively proving that the frog with its head on feels and wills. Further, if it be affirmed that sensation and volition are restricted to the brain, then the amphioxus must be without either, and that exhibited by the lower vertebrates, the frog included, out of proportion to the amount of brain present. It is often urged that, as we know from cases in which the spinal cord has been injured in man, that muscular contractions resulting from the tickling of the sole of the foot are performed unconsciously, that the muscular action just described as taking place in the decapitated frog is no evidence that the animal either feels or wills. It should be borne in mind, however, that no one ever saw a man with a fractured spine, still less with his head cut off, apply his hand or foot to his anus and wipe away acetic acid placed thereupon, as done by the decapitated frog, and until this has been observed it can hardly be said that the cases are parallel, or that conclusions can be drawn as to the sensation or volition possessed by the spinal cord of the decapitated frog from observations made upon human beings suffering from injuries of the spine by tickling the soles of the feet. Indeed, the muscular contractions following the tickling of the sole of the foot in cases of injuries of the spine in human beings are very simple in character, similar to those ensuing when the nerve of an amputated limb is stimulated, whether it be that of a man or frog.

Such contractions are never coördinated with reference to the performance of any definite object, and do not suggest in any way the idea that the amputated limb either feels or wills, and the case is not substantially altered, by the limb being attached to the body, the only difference being then that the nerve is bent into an afferent and efferent arc, the gray matter of the cord connecting the axis-cylinder of the ascending and descending parts of the same. The question may never be settled as to whether the headless frog feels and wills or not, or to what extent sensation and volition may be properties of the spinal cord in the lower vertebrates, or as to the true nature of reflex action; on the supposition, however, that man has gradually developed, and in harmony with the idea that as we pass from the lower to the higher vertebrates through the division of labor, the properties of the spinal cord from being general, become more and more special in

character, it is quite possible that many actions which are now performed unconsciously in the higher animals may have been originally accompanied with both sensation and volition in the lower ones, and to a certain extent are still. As a matter of fact, many actions like that of walking, playing upon musical instruments, etc., involving at first both sensation and volition, through constant repetition are performed in time unconsciously. Whether this view of all reflex action being originally accompanied with consciousness, but through constant repetition being finally performed unconsciously, becoming, as it were, organized within us, a kind of second nature, be accepted or not, there is no doubt that in man, at least, that the seat of sensation and volition is limited to the brain, and that there are many and varied actions going on in the body not involving consciousness at all, and performed entirely by the spinal cord and medulla, and to the consideration of which let us now turn.

A reflex action (Fig. 379) implies the presence of an afferent or centripetal nerve (*A*) of the gray matter of the cord (*C*), and of an

Fig. 379.

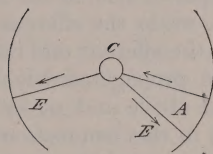
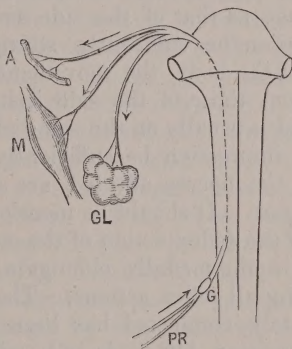


Diagram to illustrate reflex action.

Fig. 380.



efferent or centrifugal one (*E*). We make use of these terms in preference to those of sensory and voluntary motor nerves, since many reflex actions like the rhythmical action of the heart and lungs are performed entirely unconsciously without our feeling or willing in the matter at all, while others, involving sensation, as the winking of the eyelids on an object being brought suddenly close to the eyes is entirely involuntary, as we all know, from daily experience. In many instances of reflex action, as in deglutition, walking, coughing, sneezing, tetanus, vomiting, etc., both the afferent and efferent nerves involved are spinal nerves. In other cases, as in blushing, etc., while the afferent nerves are spinal, the efferent nerves belong to the sympathetic system. On the other hand, the afferent nerves may be derived from the sympathetic, the efferent from the spinal system, as in convulsions due to the presence of intestinal worms, not uncommon in infants. Finally, both afferent and efferent nerves may be sympathetic nerve fibres, as in the production of certain of the intestinal secretions. Whether, however, the afferent and efferent nerves be spinal or sympathetic in origin,



or the phenomena be accompanied with sensation, but without volition, or without either in each of the instances just referred to, an impression being made upon the periphery and transmitted by an afferent nerve to the gray matter of the cord is thence reflected outwardly again to the periphery by an efferent one, and while muscular, glandular, or vascular action may in response to an afferent irritation respectively follow, as in the instance given above, according as the efferent nerve is distributed to a muscle, gland, or vessel, it is not impossible that all three effects may be produced simultaneously by a single impression, as in Fig. 380. Many of the examples just given being rather illustrations of the reflex action of the medulla than of the spinal cord, their further consideration will be deferred until the afferent and efferent nerves involved have been described.

If the impression made upon the periphery be not a very strong one, usually the reflex action resulting is unilateral—that is to say, is confined to the same side of the body irritated. If, however, the impression be sufficiently strong to pass through the gray matter of the cord and be reflected outwardly, then the reflex action is symmetrical—that is, the general effect produced on the opposite side of the body is the same as that of the side irritated. As might be expected, if the impression be sufficiently strong to produce the same effect on both sides of the body, the movements upon the opposite side never surpass in extent those of the side irritated; further, while the efferent nerve affected is usually on the same plane as that of the afferent one irritated, if the impression be sufficiently strong to be propagated beyond the point, the nerves affected are always situated above and never below that point. It should be mentioned, however, in this connection in the case of the reflex action of the encephalon the impression passes downward to the medulla oblongata, the latter having the power of generalizing all reflex actions. That the different parts of the body are intimately connected has been well known from time immemorial to the physician, but it is only within comparatively modern times that it has been recognized that the sympathy, as it was called, undoubtedly existing between the various organs, depends upon reflex action. As the doctrine of sympathy is a very important one from a pathological as well as from a physiological standpoint, it may not appear superfluous to illustrate it a little by a few examples. Thus, for example, the œsophagus having been divided, if the stomach be irritated, the salivary glands will secrete; on the other hand, if the lingual nerve be stimulated as by the taking of tobacco, the stomach will secrete. Evidently the impression made upon the stomach in the first case is transmitted to the cord and thence reflected outwardly to the salivary glands, whereas in the second case the impression, being made upon the tongue, is transmitted to the cord and thence reflected to the stomach. Similarly the irritation due to hemorrhoids modifies the character of the gastric juice to such an extent that digestion becomes impossible, and the ensuing dyspepsia only curable by removal of the hemorrhoids or the exciting cause. The flow of tears due to some external irritation disappears with the loss of sensibility, while photophobia, often attributed to irritation of the optical nerve, is in reality due to irritation of the fifth

pair of nerves. The fact of disease in one eye often involving loss of the other illustrates the nervous sympathy existing between the two. Neuralgia of branches of the frontal nerve, due to caries of the teeth, is of frequent occurrence. The irritation, and even inflammation of the abdominal viscera following severe burns is well known to the surgeon. The stoppage of the heart brought about by blows on the epigastrium, the tetanus due to injuries of the thumb and big toe, the paraplegia from disease of the urogenital organs, the development of the mammary glands coincident with that of the foetus, are illustrations among many offered by Brown Sequard<sup>1</sup> of the important fact never to be lost sight of, that the exciting causes of many physiological and pathological phenomena are to be sought for, not where the latter are exhibited, but frequently at a remote portion of the body, the impression made upon one organ being transmitted by an afferent nerve to the spinal cord, and thence reflected outwardly by an efferent one to where the phenomena are exhibited. If the various spinal nerves involved in the production of reflex actions be considered specifically, it will be found that just as the osseous spinal column is subdivided into osseous segments, so the spinal cord may be subdivided into nervous ones physiologically at least, the gray matter of which, according to this view, constituting so many reflex centres, and the spinal nerves the afferent and efferent nerves to and from the same. Up to the present time seven such centres appear to have been satisfactorily made out.

First. The cilio-spinal centre, by which the dilatation of the pupil is effected, situated in the lower part of the cervical and upper part of the dorsal regions of the cord; it will be considered again in connection with the sympathetic. Second. The sweat centre, whose influence upon the secretion of sweat will be treated of under the skin. Third. The ano-spinal centre, governing the act of defecation, situated in the lumbar region, the afferent fibres being constituted by the hemorrhoidal and inferior mesenteric nerves, the efferent by the pudendal plexus, distributed to the sphincter ani muscle. Fourth. The vesico-spinal centre, both that governing the sphincter vesicæ and detrusor urinæ, being situated in the lumbar region of the cord. Fifth. The centre for erection of the penis, lying in the lumbar region of the cord, the afferent fibres being the sensory nerves of the penis, the efferent ones the nervi erigentes, stimulation of which, as we shall see hereafter, dilates the vessels of the penis. Sixth. The centre for the emission of semen, also situated in the lumbar region, the afferent nerves being the dorsal sensory nerves of the penis; the efferent nerve fibres, which, emerging with the fourth and fifth lumbar nerves, pass into the sympathetic, and are distributed to the vesiculæ seminales and vasa differentia, and with the third and fourth sacral nerves pass into the perineal nerves, and are distributed to the accelerator muscle. Seventh. The centre for parturition, lying in the lumbar region, the afferent and efferent fibres consisting of part of the uterine plexus. From the fact of the reflex actions being stronger, and of less time elapsing between the application of the stimulus, and the resulting reflex when the spinal cord has been

<sup>1</sup> Central Nervous System, p. 153. Philadelphia, 1860.



divided, it has been inferred that the encephalic centres exercise a restraining or inhibitory effect upon the reflex action of the cord. Thus, the spinal cord, being intact in a frog, and the average length of time elapsing between the application of the stimulus and the resulting reflex effect being determined, it will be observed that if the optic lobes, for example, be stimulated, a greater length of time elapses now than before between the stimulus and the reflex. On the other hand, the spinal cord being divided, less time elapses between the application of the stimulus and the reflex. While such experiments would lead one to conclude that the optic lobes contain a restraining or inhibitory centre, Setschenow<sup>1</sup> centre, it must not be supposed that the inhibitory influence of the encephalon is limited to the optic lobes; and further, it must be borne in mind that any reflex action would be stronger, and would take place more quickly, the cord divided, than when intact, since, under such circumstances, the whole effect of the impression made upon the periphery would appear as a reflex action, none becoming cerebral in character; whereas, the cord, being intact, part of the impression only is reflected from the cord, the remaining part being transmitted to the encephalon becoming cerebral. That there must be some internal mechanism in ourselves, by which the reflex action of the cord is inhibited, is shown by the manner in which we are able to restrain, for a time at least, the various actions performed by it.

<sup>1</sup> Ueber die Hemmungsmechanismus für die Reflexthätigkeit des Rückenmarks, 1863.

## CHAPTER XLII.

### THE MEDULLARY NERVES.

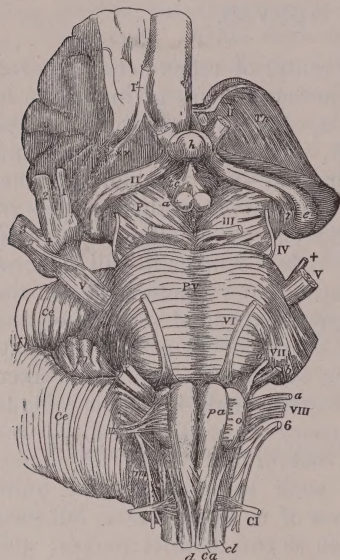
THE medulla oblongata, regarded as a centre of reflex action, is even more important than the spinal cord, on account of its giving origin to ten of the so-called cranial nerves—that is, of the nerves involved in the performance of mastication, insalivation, deglutition, of gastric and intestinal digestion, circulation, and respiration—in a word, of the functions of nutrition. In order, however, to appreciate the manner in which these nerves conduct afferent and efferent impressions to and from the medulla, the latter acting as a reflex centre, it will be first necessary to describe their origin, distribution, and function. From the fact of the medulla being simply the upper expanded portion of the spinal cord one would be led to suppose that the ten nerves originating in it would be either motor or sensory in function, and that taken together in pairs from below upward each pair would be comparable to the anterior or motor and posterior or sensory roots of one of the true spinal nerves. As a matter of fact, the roots of the two nerves of any one of the medullary pairs, supposing such to exist, do not unite together into a single nerve as in the case of a spinal nerve, but pass on separately to their ultimate distribution as two distinct nerves; and further, the reflex centres of the medulla oblongata, of which these nerves are the afferent and efferent fibres, are so fused together in man and the higher vertebrates that the primitive disposition of these centres and the relation of the nerves originating in them are no longer apparent. In fact, the union is so intimate that it is impossible to say now how many such nerves or roots there were originally, and until that is determined it will be impossible to homologize the medullary with the true spinal nerves. Indeed, until the development of the cranial nerves in the mammalia has been thoroughly worked out by the embryologist, and the relations between the cranial and spinal nerves in some of the lower vertebrates been established by the comparative anatomist, any view yet offered may be considered as based upon little more than mere speculation. The most plausible theory is that entertained by Gegenbaur,<sup>1</sup> based upon the disposition of the cephalic nerves in the shark, according to whom the third, fourth, sixth, seventh, and eighth nerves are regarded as being originally parts of the fifth nerve or trigeminal group, and the ninth, eleventh, and twelfth as parts of the tenth or the vagal group, both groups consisting of a great number of small nerves corresponding to the numerous segments of which the primitive vertebrate skull consisted, and of which but few are represented even in the skull of the sharks of the present day.

<sup>1</sup> Elements of Comparative Anatomy, trans. by F. J. Bell, p. 515. London, 1878.



Twelve pairs of nerves are given off from the base of the brain. The first two pairs, the olfactory and optic, the special nerves of the sense of smell and sight, are, as we shall see hereafter, morphologically outgrowths of the anterior cerebral vesicle; the remaining ten pairs, however, while apparently arising like the first two pairs from the base

FIG. 381.



View from below of the connection of the principal nerves with the brain. I'. The right olfactory tract. II. The left optic nerve; II'. The right optic tract; the left tract is seen passing back into *i* and *e*, the internal and external corpora geniculata. III. The left oculomotor nerve. IV. The trochlear. V. V. The large roots of the trifacial nerves. ++. The lesser roots, the + of the right side is placed on the Gasserian ganglion. 1, the ophthalmic; 2, the superior maxillary; and 3, the inferior maxillary nerves. VI. The left abducent nerve. VII. *a*, *b*. The facial and auditory nerves. *a*, VIII. *b*. The glossopharyngeal, pneumogastric, and spinal accessory nerves. IX. The right hypoglossal nerve. CI. The left suboccipital or first cervical nerve.

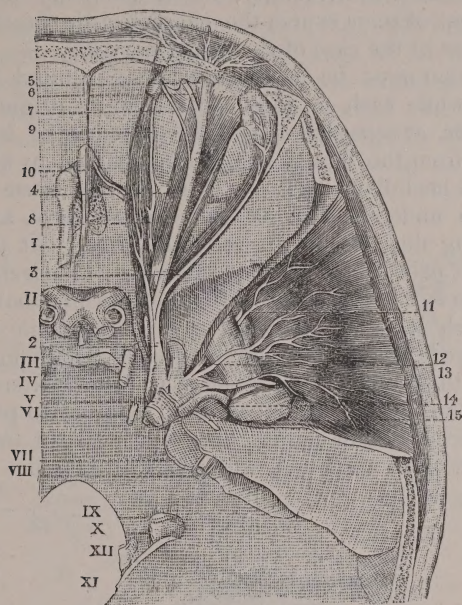
of the brain, in reality originate, as already mentioned, in the medulla, hence our reference to them as medullary nerves. Taking them in the order in which they succeed the olfactory and optic nerves, they are as follows: The third pair, or motor oculi communis; fourth pair, or patheticus; fifth pair, or trigeminal or trifacial; sixth pair, or abducent; seventh pair, or facial; eighth pair, or auditory, the special nerve of the sense of hearing; ninth pair, glosso-pharyngeal; tenth pair, pneumogastric; eleventh pair, spinal accessory; twelfth pair, hypoglossal. The third nerve or motor oculi communis (Fig. 381 and 382, III) consisting of about 15,000 fibres,<sup>1</sup> arises from a nucleus of multipolar cells situate beneath the gray fibres of the aqueduct of Sylvius, beneath the corpora quadrigemina, and extends beneath the upper part of the fourth ventricle, the fibres of the nerves decussating at their origin. From this nucleus the fibres pass forward through the crus, emerging at the base of the brain from the inner surface of the crura cerebri immediately in front of the pons. As the nerve passes through the sphenoidal fissure into the orbit (Fig. 383) it divides into two branches, the superior and smaller branches supplying the superior rectus and levator palpebræ superioris muscles, the inferior and larger branch the internal

and inferior recti and the superior oblique muscles. The latter or inferior branch gives off also a short, thick filament, which passing into the ophthalmic ganglion of the sympathetic is supposed, as we shall see, to pass thence as the short ciliary nerves into the iris, innervating the circular muscular fibres of the latter. During its course the fibres of the third pair run in common or in juxtaposition with fibres derived from the ophthalmic division of the fifth pair, and

<sup>1</sup> Rosenthal: De Numero atque Mensura Microscop Fibrillarum. Breslau, 1845.

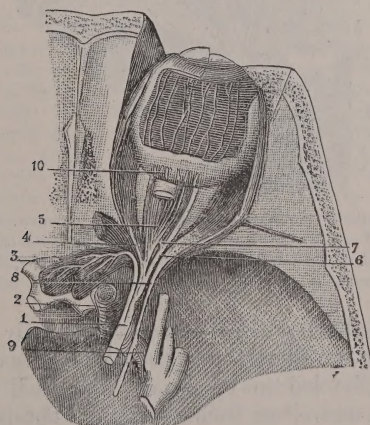
from the cavernous plexus of the sympathetic. We make use of the expression running in company with, or in juxtaposition with, in

FIG. 382.



Roots of the cranial nerves. I. First pair; olfactory. II. Second pair; optic. III. Third pair; motor oculi communis. IV. Fourth pair; patheticus. V. Fifth pair; nerve of mastication and trifacial. VI. Sixth pair; motor oculi externus. VII. Facial. VIII. Auditory—Seventh pair. IX. Glosso-pharyngeal. X. Pneumogastric. XI. Spinal accessory—Eighth pair. XII. Ninth pair; sublingual. The numbers 1 to 15 refer to branches which will be described hereafter. (HIRSCHFELD.)

FIG. 383.



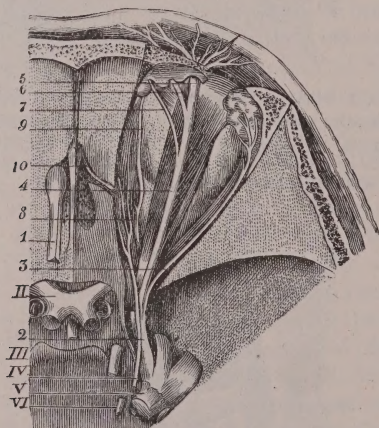
Distribution of the motor oculi communis. 1. Trunk of the motor oculi communis. 2. Superior branch. 3. Filaments which this branch sends to the superior rectus and the levator palpebræ superioris. 4. Branch to the internal rectus. 5. Branch to the inferior rectus. 6. Branch to the inferior oblique muscle; 7. Branch to the lenticular ganglion. 8. Motor oculi externus. 9. Filaments of the motor oculi externus anastomising with the sympathetic. 10. Ciliary nerves. (HIRSCHFELD.)



preference to that of anastomosis, etc., since the various medullary nerves do not actually receive fibres from or anastomose with each other in the sense that arteries and veins anastomose. The nerves, in fact, never lose their individuality, but undoubtedly preserve through the whole extent of their course the characteristic functions obtaining at their roots, as in the case of the spinal nerves.

This distinction must be continually borne in mind, for, as we shall see presently, while each of these nerves, at its origin, has a definite function—motor, or sensory—they become, sooner or later, apparently mixed nerves, from the fact of being accompanied by the fibres of the adjacent cranio-medullary nerves. It is in this sense that the third nerve is to be understood as being a motor nerve, any evidences of sensibility being due, not to its intrinsic fibres, but to the extrinsic ones of the fifth pair. That the third nerve is exclusively a motor nerve is shown by the fact of irritation of the root causing contractions of the muscles to which it is distributed, but no pain, while division of the nerve is followed by paralysis of the same.<sup>1</sup> Pathological facts, like the falling of the upper eyelid, or blepharoptosis, external strabismus, immobility of the eye, except outwardly; inability to rotate the eye on its antero-posterior axis in certain directions; slight protrusion of the eyeball; dilatation of the pupil, with some interference with the move-

FIG. 384.



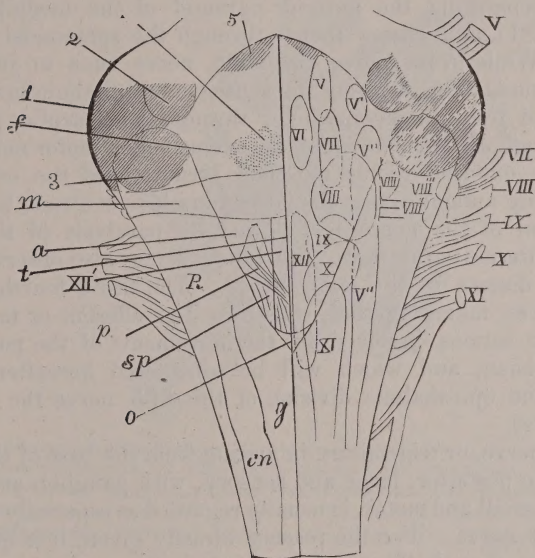
Distribution of the patheticus. *I.* Olfactory nerve. *II.* Optic nerves. *III.* Motor oculi communis. *IV.* Patheticus, by the side of the ophthalmic branch of the fifth, and passing to the superior oblique muscle. *VI.* Motor oculi externus. 1. Ganglion of Gasser. 2, 3, 4, 5, 6, 7, 8, 9, 10. Ophthalmic division of the fifth nerve, with its branches. (HIRSCHFELD.)

ments of the iris, following disease of the third pair in man, are among the proofs that may be offered that the third pair of nerves is in man motor, as we would be led to suppose it would be, both from its anatomical distribution as well as from the results obtained by vivisection.

<sup>1</sup> Mayo: *Anatomical and Physiological Commentaries*, p. 5. London, 1823. *Outlines of Human Physiology*, p. 294. London, 1827. Bernard: *Système nerveux*, tome ii. p. 204. Paris, 1858. Chauveau: *Journal de physiologie*, tome v. p. 274. Paris, 1862. Longet: *Physiologie*, tome iii. p. 554. Paris, 1869.

The fourth nerve, or patheticus, consisting of about 1100 fibres, arises in the valve of Vieussens. The fibres, after decussating at their origin, emerge at the base of the brain (Figs. 381, 382, iv), as comparative slender filaments at the sides of the pons, and, winding around the crura, pass through the sphenoidal fissure (Fig. 384) into the orbit, and supply the superior oblique muscle. Irritation of the nerve in a living animal, at its origin, causes contraction of the superior oblique muscle, and division of the nerve paralysis of the same.<sup>1</sup> In cases where the nerve is diseased in man, paralysis of the superior oblique muscle is observed as well as immobility of the eyeball, so far as rotation is con-

FIG. 385.



View of the posterior surface of the medulla, the roof of the fourth ventricle being removed to show the rhomboid sinus clearly. The left half of the figure represents: *Cn*. Funiculus cuneatus, and *g*, funiculus gracilis. *O*. Obex. *sp*. Nucleus of the spinal accessory. *p*. Nucleus of pneumogastric. *p+sp*. Ala cinerea. *R*. Restiform body. *XII'*. Nucleus of the hypoglossal. *t*. Funiculus teres. *a*. nucleus of the acoustics. *m*. Striae medullares. 1, 2, and 3 Middle, superior, and inferior cerebellar peduncles respectively. *f*. Fovea anterior. 4. Eminentia teres (genu nervi facialis). 5. Locus coeruleus. The right half of the figure represents the nerve nuclei diagrammatically: *V*. Motor trigeminal nucleus. *V'*. Median and *V''*, inferior sensory and trigeminal nuclei. *VI*. Nucleus of abducens. *VII*. Facial nucleus. *VIII*. Posterior median acoustic nucleus. *VIII'*. Anterior median. *VIII''*. Posterior lateral. *VIII'''*. Anterior lateral acoustic nuclei. *IX*. Glosso-pharyngeal nucleus. *X*, *XI*, and *XII*. Nuclei of vagus, spinal accessory, and hypoglossal nerves respectively. The Roman numerals at the side of the figure, from *V*. to *XII*., represent the corresponding nerve roots. (ERR.)

cerned, and, when the eye is moved toward the shoulder, we have double vision, the eye not rotating to maintain the globe in the same relative position. The pathological facts observed in man, as well as the anatomical distribution, confirm the view based upon vivisections, that the fourth nerve is exclusively motor at its origin, any sensibility

<sup>1</sup> Longet, op. cit., tome iii. p. 557. Chauveau, op. cit., tome v. p. 275.



it may possess further on in its course being due to adjacent filaments from the ophthalmic branches of the fifth pair, or the sympathetic.

The sixth nerve, the abducens, or motor oculi externus, being, like the fourth nerve, distributed to a single muscle, the external rectus, and, therefore, exclusively motor in function, will be considered now before the fifth nerve, which would, otherwise, be the next in order. The sixth, consisting of from 2000 to 2500 fibres, arises from a nucleus of large multipolar cells, situated beneath the eminentia teres, in the middle of the floor of the fourth ventricle (Fig. 385, vi). Unlike the fibres of the third and fourth pairs, it has not yet been shown that the fibres of the sixth nerve decussate at their origin in the floor of the fourth ventricle. The sixth nerve appears at the base of the brain in the groove separating the anterior pyramid of the medulla from the pons (Fig. 381), and passes thence through the sphenoidal fissure into the orbit. While in its course the sixth nerve runs in juxtaposition with the filaments derived from the sensitive ophthalmic branch of the fifth pair, and from the sympathetic through the carotid plexus, and Meckel's ganglion. It is undoubtedly exclusively a motor nerve, supplying only the external rectus muscle. Irritation of the nerve at the root in a living animal causes the latter muscle to contract, but no pain, while division of the nerve is followed by paralysis of the external rectus and internal strabismus,<sup>1</sup> the latter being also observed in man in cases of disease of the sixth nerve. The third, fourth, and sixth pairs of nerves, taken together, constitute the efferent or motor nerves in the reflex actions involved in the movements of the pupil and the eyeball in vision, and which will be considered hereafter, the optic nerve and the ophthalmic division of the fifth nerve the afferent or sensory nerves.

The fifth nerve, or trigeminus, in arising from the base of the brain by two roots, the posterior, large and sensory, with ganglion attached, and the anterior, small and motor, is usually regarded as especially comparable with a spinal nerve. For the reasons already given, it is quite as possible, however, that the fibres of the third, fourth, and even of the sixth nerves, may constitute the true motor fibres corresponding to the sensory fibres of the fifth (ophthalmic and superior maxillary) as that the fibres of its small motor root should be so especially regarded, particularly as the latter, as we shall see presently, are distributed exclusively in company with the fibres of the inferior maxillary branch of the fifth.

The two roots, both large and small, of which the fifth nerve actually consists without any reference to their morphological significance, arise by decussating fibres in the cells situated in the outer angle of the floor of the fourth ventricle (Fig. 385, v v' v''); passing thence separately forward and upward through the substance of the pons, they emerge from the upper border of the side of the latter (Fig. 381, v). The posterior large or sensory root, consisting of about 30,000 fibres, passes thence into the Gasserian or semilunar ganglion (Fig. 381, +), situated in the depression on the internal portion of the anterior face of the petrous portion of the temporal bone, which subdivides into the ophthalmic superior

<sup>1</sup> Longet, op. cit., tome iii. p. 560. Chauveau, op. cit., tome v. p. 275.

maxillary and inferior maxillary nerves (Fig. 386), hence its name, tri-facial. The anterior small or motor root, consisting of about 10,000 fibres, passes underneath the ganglion of Gasser, from which it occa-

FIG. 386.



General plan of the branches of the fifth pair. 1. Lesser root of the fifth pair. 2. Greater root passing forward into the Gasserian ganglion. 3. Placed on the bone above the ophthalmic nerve, which is seen dividing into the supraorbital, lachrymal, and nasal branches, the latter connected with the ophthalmic ganglion. 4. Placed on the bone close to the foramen rotundum, marks the superior maxillary division. 5. Placed on the bone over the foramen ovale, marks the submaxillary nerve. (After a sketch by CHARLES BELL.)  $\frac{1}{3}$ .

sionally receives a few filaments, and lying behind the inferior maxillary branch of the large root, passes through the foramen ovale in company with the latter, with which it is finally distributed. It will be observed that while the ophthalmic and superior maxillary branches of the fifth are purely sensory, being derived solely from the large root through the Gasserian ganglion, the inferior maxillary branch is both motor and sensory, being derived not only from the ganglion but from the small or motor root as well. It may be appropriately mentioned here, with reference to certain effects following division of the fifth nerve to be mentioned presently, that the ganglion of Gasser receives filaments from the sympathetic. While it is an extremely difficult operation if not impossible, to stimulate the small root of the fifth nerve in a living animal, nevertheless, there can be little doubt that it is a purely motor nerve in function, since if it be stimulated in an animal just dead, in which the cerebral lobes have been removed, such of the muscles of mastication as are supplied by the fibres of the small root (running in



the inferior maxillary division of the fifth) at once contract,<sup>1</sup> and in the case of old horses, for example, with such force as to break off pieces of the teeth<sup>2</sup>, no such result following stimulation of the large root.

In division of the nerve in a living animal with the view of determining its function<sup>3</sup> both roots are necessarily divided, and with the complete loss of sensibility ensuing under such circumstances, there is also observed paralysis of the temporal, masseter, internal and external pterygoid, mylohyoid, and anterior belly of the digastric muscles, or the muscles of mastication supplied by the fibres of the small root running in the inferior maxillary division of the fifth nerve and of the tensor muscles of the velum palati. The effect of division of the fifth nerve is very striking in the case of the rabbit, in which, through the consequent paralysis of the muscles of mastication, the line of contact between the incisor teeth becomes oblique instead of horizontal, the incisor teeth being worn away unevenly through the jaw being drawn to one side by the action of the active muscles. The cases of paralysis of the fifth nerve that have been noted in man confirm in the main the results of experiments made upon animals. In all instances where both the large and small roots were involved by the disease, entire loss of sensibility and paralysis of the muscles supplied by the fifth were observed,<sup>4</sup> the only cases in which there was no paralysis of the muscles of mastication being those in which the small root was unaffected, loss of sensibility on the side affected being then only noted. In order to appreciate the results following division of the large root of the fifth nerve in a living animal or disease in man, it will be first necessary to describe briefly the distribution of its principal branches. It has already been mentioned that the large root after expanding into the ganglion of Gasser subdivides into the ophthalmic superior and inferior maxillary nerves. The ophthalmic, the smallest of the three branches of the large root, passes through the sphenoidal fissure into the orbit, subdividing into the lachrymal, frontal, and nasal nerves, and gives off, during its course to the orbit, fibres to the third, fourth, and sixth nerves, to the tentorium and to the sympathetic. The lachrymal nerve supplies the lachrymal gland, conjunctiva, integument of the upper eyelid, and gives off fibres to the orbital branch of the superior maxillary. The frontal branch divides into the supratrochlear and supraorbital nerves, the former nerve supplies the integument of the forehead and gives off a long, delicate filament to the nasal nerve; the latter, or supraorbital nerve, passing through the supraorbital foramen supplies, to a certain extent, the upper eyelid and forehead, the anterior and median portions of the scalp, the mucous membrane of the frontal sinus, and the pericranium covering the frontal and parietal bones.

The nasal branch, before entering the orbit, gives off a long filament to the ophthalmic ganglion, and then the long ciliary nerves supplying the ciliary muscle, iris, and cornea; it then divides into the external nasal, or infra-trochlearis, and the internal nasal, or ethmoidal nerves.

<sup>1</sup> Longet: *Anatomie et physiologie du système nerveux*, tome ii. p. 190. Paris, 1842. *Physiologie*, op. cit., p. 562.

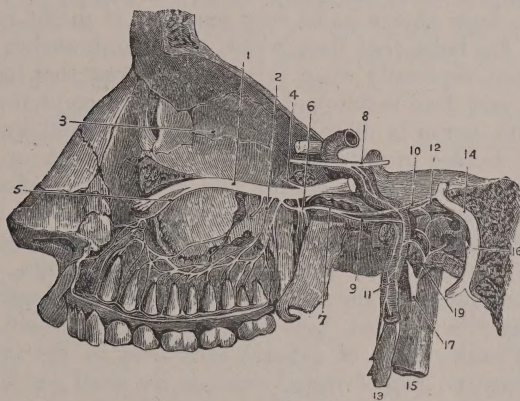
<sup>2</sup> Chauveau, op. cit., p. 276.

<sup>3</sup> Bernard: *Système Nerveux*, tome ii. p. 100. Paris, 1858.

<sup>4</sup> Longet: *Anat. et Phys. du système nerveux*, tome ii. p. 191. Paris, 1842.

The infra-trochlearis nerve supplies the integument of the forehead and nose, the internal surface of the lower eyelid, the lachrymal sac, and caruncula. The internal nasal, or ethmoidal nerve, supplies the mucous membrane of the nose, and partly its integument. The second branch of the fifth nerve, the superior maxillary nerve (Fig. 387), passes out of the cranium by the foramen rotundum, and traversing the infraorbital canal emerges by the infraorbital foramen upon the face, giving off palpebral branches to the lower eyelid, nasal branches to the side of the nose, the latter running in common with the nasal branch of the ophthalmic and labial branches to the integument and mucous membrane of the upper lip. During its course through the speno-maxillary fossa the superior maxillary nerve gives off several branches; the orbital, which, passing into the orbit, gives off, in turn, the temporal and malar nerves, which, emerging by foramina in the malar bones, are distributed to the integument of the temple and side of the forehead, and the integument covering the malar bone respectively, the two posterior dental nerves (Fig. 387), the latter supplying the molar and bicuspid teeth,

FIG. 387.



Dissection of the superior maxillary nerve and Meckel's ganglion. 1. Superior maxillary nerve. 2. Posterior dental nerves. 3. Inner wall of orbit. 4. Orbital branch (cut). 5. Anterior dental nerve. 6. Meckel's ganglion. 7. Vidian nerve. 8. Sixth nerve. 9. Carotid branch of Vidian. 10. Greater superficial petrosal nerve. 11. Carotid plexus of sympathetic. 12. Lesser superficial petrosal nerve. 13. Superior cervical ganglion of sympathetic. 14. Facial nerve. 15. Internal jugular vein. 16. Chorda tympani nerve. 17. Glosso-pharyngeal nerve. 19. Jacobson's nerve. (From HIRSCHFELD and LEVEILLÉ.)

the mucous membrane of the alveolar processes and of the antrum. In the infraorbital canal the anterior dental is given off, constituting, together with the posterior dental, the dental arcade, the anterior dental supplying the canine and incisor teeth, and the mucous membrane of the alveolar processes. The third branch of the fifth nerve, or the inferior maxillary (Fig. 386), passes out of the cranial cavity by the foramen ovale, and after uniting with the small or motor root of the fifth, divides into anterior and posterior branches, the former containing the motor fibres supplying the principal muscles of mastication, and the tensor muscles of the velum palati through the otic ganglion, and derived, as



already mentioned, from the small or motor root, the latter containing principally sensory fibres. Among the most important of these may be mentioned the auriculo-temporal, the lingual, and the inferior dental nerves. The auriculo-temporal nerve supplies the integument of the temporal region, of the ear, the auditory meatus, the temporo-maxillary articulation, and the parotid gland; it gives off, also, filaments that run in common with those of the seventh nerve, or facial. The lingual nerve, distributed to the mucous membrane of the point of the tongue, mouth, gums, sublingual gland, submaxillary ganglion, consists, as we shall see, through a considerable extent of its course, of two distinct nerves, the lingual proper and the chorda tympani, and whose relations will be considered presently. The inferior dental nerve, after giving off the mylohyoid nerve, passes through the dental canal in the inferior maxillary bone, and supplying the lower teeth, emerges upon the face at the mental foramen, and, as the mental nerve, supplies the integument of the chin, the lower part of the face, and lower lip, and partly the mucous membrane of the mouth. While, as already mentioned, it is impossible to stimulate directly the large root of the fifth nerve in a living animal, yet, since all of its accessible branches, both in man and animals, have been shown to be very sensitive, it might reasonably be inferred that the large root from which all these branches arise is sensory in function, especially when it is remembered that its stimulation in an animal just dead is followed by no contractions of the muscles to which the fifth nerve is distributed. Further, as well known,<sup>1</sup> if the large root be divided in a living animal, or be injured or diseased in man, entire loss of sensibility on the side of the head affected at once follows, any muscular paralysis ensuing being limited to the parts supplied by the fibres of the small or motor root. The immediate effect of division of the large root is very striking, the cornea, integument, and mucous membrane of the side affected are at once deprived of sensibility, and may be burned, lacerated, or pricked without the animal evincing any pain. Loss of general sensibility in the tongue is also observed, though no loss of taste,<sup>2</sup> since, as we shall see hereafter, the gustatory properties of the anterior part of the tongue are due to the chorda tympanic fibres of the lingual nerve, and not to those fibres of the lingual proper derived from the inferior maxillary branch of the fifth nerve. Deglutition becomes impossible, also, on the side of the head affected.

The loss of general sensibility, the interference with deglutition, etc., are also observed in paralysis of the fifth nerve occurring in human beings. In one of these cases,<sup>3</sup> it may be mentioned as a proof of the sensory properties of the large root of the fifth nerve, that an operation was performed without the slightest evidence of pain on the part of the patient. In addition to the loss of sensibility, etc., following division of the large root of the fifth nerve, in certain cases of inflammation of the eye, ear, and nose have also been observed, depending apparently

<sup>1</sup> Magendie: *Journal de Physiologie*, tome iv. pp. 176, 302. Paris, 1824. Bernard: *Leçons: Sur la physiologie et la pathologie du Systeme nerveux*, tome ii. p. 53. Paris, 1858.

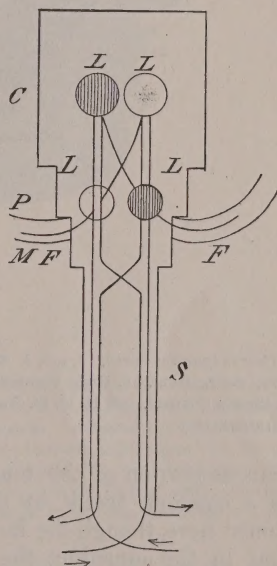
<sup>2</sup> Schiff: *Leçons sur la physiologie de la digestion*, tome i. p. 103. Florence, 1867. Lusanna: *Archives de Phys.*, tome ii. p. 27. Paris, 1869.

<sup>3</sup> Noyes: *New York Med. Journal*, 1871, vol. xiv. p. 163.

upon division of those fibres of the sympathetic, already alluded to, as passing into the ganglion of Gasser, since it is only when these fibres are involved through division of the large root through the ganglion, or anterior to it, that such effects are noticed, none such following if the large root be divided between its origin and the ganglion. In the former—that is, where the sympathetic fibres have been divided within from about one to two days after the operation—the eye on the side affected becomes the seat of purulent inflammation; the cornea, after becoming opaque, ulcerates, the humors of the eye are discharged, and the organ destroyed. Ulcers also appear upon the tongue and lips, and there is a discharge from the mucous membrane of the nose and mouth, and the hearing appears to be affected. The impairment in the nutrition of the eye, mouth, etc., following division of the fifth nerve, and of the fibres of the sympathetic, appears to be due, both to the hyperæmia induced through the division of the vasomotor fibres of the sympathetic, and which, we shall see hereafter, regulate the calibre of the bloodvessels, and to the paralysis of the muscles of mastication, and consequent imperfect digestion of food, the increased vascularity and consequent exaggerated nutrition necessitating a greater amount of nutritive matter; in the diminution of the latter, the parts involved become inflamed. That such is the true explanation, to a considerable extent, is shown from the fact that the inflammation of the eye, etc., can be prevented, for some weeks at least, if the animal be artificially fed with good nutritive food. It need hardly be mentioned that the nervous fibres transmitting gustatory, olfactory, and auditory impressions are not in any way derived from the large root of the fifth nerve, as once thought, the large root being only a nerve of general sensibility, the small root of motion.

The seventh nerve, the nerve of expression, the facial, or the portio dura of the seventh pair, supposing the latter to include, as in the arrangement of Willis, not only the fibres of the facial proper, but those of the auditory, or portio mollis, containing about 4500 fibres, arises in a fan-shaped manner in the gray matter of the floor of the fourth ventricle (Fig. 385, vii). Pathological cases, like these observed, particularly by Gubler,<sup>1</sup> lead one to conclude that the fibres of the facial decussate, not only at their apparent origin in the floor of the fourth ventricle, but that many of them, passing upward, decussate in the pons Varolii. At least, it is only on such a supposition that cases of so-called alternate paralysis can be explained, in which (Fig. 388),

FIG. 388.



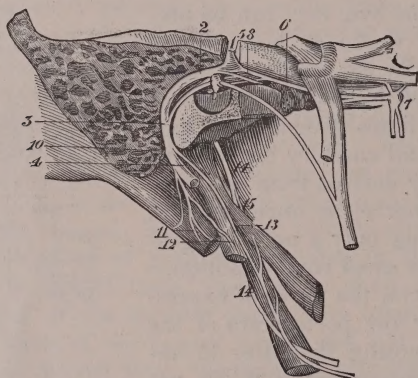
To illustrate alternate paralysis. C. Cerebrum. P. Pons. M. Medulla. F. Facial. L. Lesion, spinal cord.

<sup>1</sup> Gazette hebdomadaire de médecine et Chirurgie. Paris, 1856, 58, 59.



while a lesion of the brain, situated anterior to the pons, is associated with facial paralysis on the same side as that of the accompanying hemiplegia, a lesion situated in the pons, or below it, is accompanied with a facial paralysis on the opposite side to that of the hemiplegia. It must be admitted, however, that, as yet, no such decussating fibres as those just supposed to exist as accounting for the pathological phenomena, have been actually demonstrated by the anatomist. The fibres of the facial nerve, from their origin in the fourth ventricle, passing forward and outward through the medulla, emerge from the latter at the lower border of the pons Varolii in the outer part of the depression between the olivary and the restiform bodies (Fig. 381, vii), the auditory nerve lying to the outer side of the facial, the two being not infrequently connected by a separate fasciculus of the facial, the so-called *pars intermedia*, or nerve of Wrisberg. After emerging from the medulla, the facial, the auditory, and the intermediary nerves, if the latter exists, pass thence together into the internal auditory meatus. The further distribution and origin of the auditory nerve will be considered hereafter; leaving the latter nerve, then, for the present, at the bottom of the meatus, the facial and nerve of Wrisberg will be found to enter the aquæductus Fallopii (Fig. 389), and passing, by this route, through the

FIG. 389.



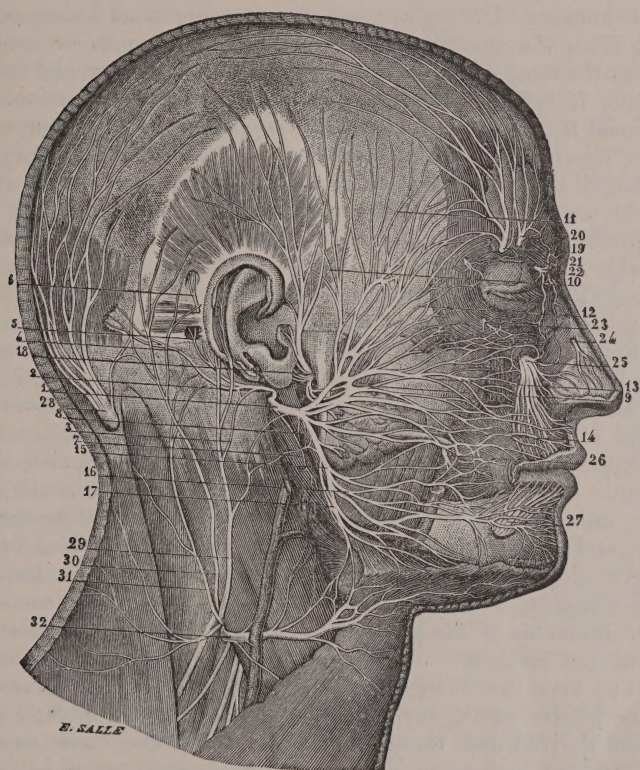
Chorda tympani nerve. 1, 2, 3, 4. Facial nerve passing through the aquæductus Fallopii. 5. Gangliform enlargement. 6. Great petrosal nerve. 7. Spheno-palatine ganglion. 8. Small petrosal nerve. 9. Chorda tympani. 10, 11, 12, 13. Various branches of the facial. 14, 15. Glossopharyngeal nerve (HIRSCHFELD.)

petrous portion of the temporal bone, the two nerves uniting, emerge as a common trunk by the stylo-mastoid foramen. It may be mentioned here, though the fact has, as yet, but little functional significance, that in the aquæduct the nerve of Wrisberg exhibits a little reddish ganglion, containing nerve cells. The most important branches of the facial are briefly as follows: The large and small petrosal nerves passing, respectively, to Meckel's and the otic ganglia (Fig. 389), the external petrosal to the sympathetic fibres of the middle meningeal artery, the tympanic branch distributed to the stapedius muscle, the chorda tympani nerve (Fig. 389) passing through the tympanum

to join the lingual branch of the inferior maxillary, the branch to the pneumogastric.

The six branches just mentioned are given off by the facial during its course through the aqueduct of Fallopius. The remaining branches still to be mentioned are given off after the nerve has emerged from the stylo-mastoid foramen, the branch to the glosso-pharyngeal nerve, the posterior auricular connected with the cervical plexus by the auricularis

FIG. 390.



Superficial branches of the facial and the fifth. 1. Trunk of the facial. 2. Posterior auricular nerve. 3. Branch which it receives from the cervical plexus. 4. Occipital branch. 5, 6. Branches to the muscles of the ear. 7. Digastric branches. 8. Branch to the stylo-hyoid muscle. 9. Superior terminal branch. 10. Temporal branches. 11. Frontal branches. 12. Branches to the orbicularis palpebrarum. 13. Nasal, or suborbital branches. 14. Buccal branches. 15. Inferior terminal branch. 16. Mental branches. 17. Cervical branches. 18. Superficial temporal nerve (branch of the fifth). 19, 20. Frontal nerve (branches of the fifth). 21, 22, 23, 24, 25, 26, 27. Branches of the fifth. 28, 29, 30, 31, 32. Branches of the cervical nerves. (HIRSCHFELD.)

magnus and distributed to the retrahens and attolens aurem, the occipital portion of the occipito-frontalis muscle, and the integument, the digastric branch receiving filaments from the glosso-pharyngeal supplying the posterior belly of the muscle of the same name and the stylo-hyoid, a distinct branch also to the stylo-hyoid muscle, the lingual branch—that is, the branch passing behind the stylo-pharyngeus muscle and receiv-



ing filaments from the glosso-pharyngeal nerve to be distributed to the mucous membrane, tongue, stylo-glossus, and palato-glossus muscles, and, finally (Fig. 390), the temporo-facial and cervico-facial branches into which the main trunk divides as it passes through the parotid gland. The temporo-facial branch passing upward and forward is distributed to the *attrahens aurem*, the frontal portion of the *occipito-frontalis*, the *orbicularis palpebrarum*, *corrugator supercilii*, *pyramidalis nasi*, *levator labii superioris*, *levator labii superioris*, *alæque nasi*, the *dilator* and *compressor nasi*, part of the *buccinator*, the *levator anguli oris*, and the *zygomatic* muscles. During its course the temporo-facial branch receives filaments from the auriculo-temporal branch of the inferior maxillary nerve from the temporal branch of the superior maxillary and from the ophthalmic, it becomes, therefore, a mixed nerve in function. The cervico-facial nerve, passing downward, supplies the *buccinator*, *orbicularis oris*, *risorius*, *levator labii inferioris*, *depressor labii inferioris*, *depressor anguli oris*, and *platysma myoides*. From the fact that division of the fifth nerve is at once followed by entire loss of sensibility in the parts supplied by that nerve, it is evident that the facial, supplying to a considerable extent identical regions, cannot be a sensory nerve, otherwise sensibility, though weakened, should nevertheless persist in the face, etc., even after division of the fifth nerve. Direct evidence, however, as well as indirect, proves conclusively that the seventh nerve, at its origin at least, is a purely motor nerve. Thus, division of the nerve in a living animal or disease in man is at once followed by paralysis of the facial and other muscles that we have just seen are supplied by the nerve, while stimulation of the nerve at its root in a living animal or in one recently dead, causes contraction of the muscles, but in the case of the living animal no pain. Any sensibility then exhibited by the facial nerve beyond its root must be attributed to the fibres derived from the fifth nerve, glosso-pharyngeal, and pneumogastric, that we have seen run in juxtaposition with it. In order to appreciate the varied and important functions of the facial nerve, it will be best to consider those of its branches *seriatim*. In the consideration of the sympathetic, to be taken up hereafter, it will be then shown that the nerve fibres supplying the *levator palati*, *azygos uvulæ*, *palato-pharyngeus*, and *palato-glossus* are derived from the ganglion of Meckel, and those supplying the *tensor palati* and *tensor tympani* from the otic ganglion; and on the supposition that the great and small petrosal nerves pass respectively through the two ganglia to the muscles just mentioned, supplied by the latter, it might be inferred that paralysis of the facial nerve would be accompanied with difficulty in deglutition and an increased sensitiveness to sound, the tympanic membrane being relaxed through the paralysis of the *tensor-tympani* muscle, it being well known that the tympanic membrane<sup>1</sup> vibrates more intensely when relaxed than when tensed. Pathological cases of facial paralysis occurring in man fully confirm this view, since in such cases both difficulty in deglutition and increased susceptibility to sounds, etc., are observed.<sup>2</sup> Further, as confirming the

<sup>1</sup> Muller's Elements of Physiology, vol. ii. p. 1256. London, 1843.

<sup>2</sup> Bell: The Nervous System, p. 329. London, 1844. Bernard: Leçons sur la physiologie et la pathologie du système nerveux, tome ii. pp. 114, 133. Paris, 1858. Montanet: Dissertation sur l'hémiplégie faciale. These No. 300. Paris, 1831.

view that the muscles of deglutition are supplied by the facial, may be mentioned the fact of the facial nerve giving off the branch already alluded to supplying the stylo-glossus and palato-glossus muscles, and occasionally of the branch distributed to the palato-glossus and palato-pharyngeus muscles passing directly to the latter without being connected with the glosso-pharyngeal, as is usually the case.<sup>1</sup> The chorda tympani nerve, one of the most remarkable nerves in the body, both on account of its origin and distribution as well as of its properties, is usually said to arise from the facial in the aqueduct of Fallopius and passing through the canal of Huguier into the tympanum, to cross the latter between the malleus and incus, to enter the Gasserian fissure, emerging thence to join the lingual nerve at the acute angle (Fig. 389). In the horse and calf, however, as shown by Owen<sup>2</sup>, the chorda tympani nerve, while apparently arising from the facial, as in man, in reality can be traced through the fibres of the facial as a continuation of the large petrosal, and as the latter nerve is connected through the ganglion of Meckel with the superior maxillary nerve a pathway evidently exists in these animals by which the impressions made upon the tongue can be transmitted to the latter nerve, and while the chorda tympani nerve has not been actually demonstrated in man to be a continuation of the large petrosal, as in Fig. 391, both experiments upon animals and pathological cases in man lead one, as we shall see, to suppose that such is substantially the case. On the other hand, apart from the fact of nerve fibres not anastomosing, there is direct experimental evidence to show that the chorda tympanic fibres do not lose their individuality after joining those of the lingual branch of the inferior maxillary, but preserve their functional activity entirely independent of those of the latter. Thus, if the lingual branch of the inferior maxillary be divided before it is joined by the chorda tympani, its fibres alone atrophy, with ensuing loss of general sensibility of the anterior part of the tongue, whereas, if the chorda tympani nerve be divided before it reaches the lingual its terminal fibres alone atrophy, loss of taste ensuing.

Experiment not only shows, however, that the terminal portion of the lingual nerve consists of fibres derived from both the lingual branch of the inferior maxillary, and from the chorda tympani, but that the latter consists of three distinct sets of fibres: 1st, those endowing the anterior two-thirds of the tongue with the sense of taste; 2d, those modifying the bloodvessels of the tongue, vasa dilator nerves; 3d, those stimulating through the submaxillary ganglion the submaxillary and sublingual glands. The chorda tympani nerve, consisting, as it undoubtedly does, then, of sensory, motor, and secretory fibres, it is to be expected

FIG. 391.

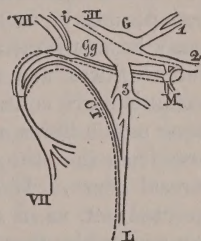


Diagram to illustrate supposed connection of chorda tympani with superior maxillary through facial, great petrosal, and ganglion of Meckel.

<sup>1</sup> Longet, op. cit., tome iii. p. 581.

<sup>2</sup> The Anatomy of Vertebrates, vol. iii. p. 156. London, 1868.



that it should have specifically different centres of origin, which is in harmony with the view just offered of its motor fibres being derived from the facial, and its sensory fibres from the superior maxillary nerve through the large petrosal and the ganglion of Meckel. That the chorda tympani nerve does contain at least some fibres derived from the superior maxillary appears from the fact of paralysis of the fifth nerve in man being often accompanied with loss of the sense of taste in the anterior portion of the tongue,<sup>1</sup> and that these gustatory fibres are a continuation of those of the large petrosal is still further confirmed by another fact, that paralysis of the seventh nerve involves equally as well as that of the fifth nerve, loss of the sense of taste in the tongue.<sup>2</sup> The further consideration of the gustatory and vaso-dilator fibres of the chorda tympani will be deferred for the present. Inasmuch, however, as those fibres of the chorda tympani that pass to the submaxillary ganglion and sublingual glands constitute the efferent fibres in the reflex mechanism of insalivation as effected by those glands, the fibres of the lingual branch of the inferior maxillary, together with those of the glosso-pharyngeal and pneumogastric, the afferent fibres, and the medulla the centre; their function, in this connection, may be appropriately here considered, and, to avoid repetition, it may be mentioned that, in the case of the parotid gland, while the afferent fibres are the same, the efferent fibres involved in the reflex mechanism are contained in the auriculo-temporal branch of the fifth, whose motor fibres are derived from the small or motor root, and in the fibres from the otic ganglion derived from the facial, through the small petrosal nerve. If the submaxillary and sublingual glands be cleanly dissected out, as in a living dog, for example, in which the glands are very accessible, they will be seen to be comparatively at rest, secreting little or no saliva, and their venous blood of a dark hue. If now a drop of vinegar be placed upon the tongue of the animal, at once the arterial twigs enlarge, the blood flows more rapidly, the veins pulsate, the color of their blood becomes scarlet, and the pressure increases, followed by an abundant discharge of limpid, very alkaline saliva, the so-called chorda tympani saliva, containing small quantities of albumen, globulin, mucin. That the phenomena just described are due to impressions transmitted to the medulla by the afferent sensory fibres of the lingual branch of the inferior maxillary and glosso-pharyngeal nerves, and thence reflected back to the submaxillary and sublingual glands by the efferent secreto-motor fibres of the chorda tympani, is shown by such facts as that, after division of the lingual branch, the secretion of saliva, etc., ceases, but recommences if the central end of the divided nerve be stimulated. On the other hand, if the chorda tympani be divided, the vessels supplying the submaxillary and sublingual glands contract; owing to the unopposed action of the sympathetic vaso-constricting fibres, the blood flows slowly, is diminished in quantity, and becomes dark, the secretion of saliva diminishes; the application of vinegar no longer excites the secretion. That the secretion does not altogether cease after division of the chorda tympani

<sup>1</sup> Schiff: *Leçons sur la Physiologie de Digestion*, tome premier, p. 100. Florence and Turin.

<sup>2</sup> Bernard: *Système Nerveux*, 1858, tome ii. p. 122. Schiff, *op. cit.*, tome i. p. 183. Lusanna: *Archives de Physiologie*, tome ii. p. 201. Paris, 1869.

appears to be due to the independent reflex action of the submaxillary ganglion. If now, however, the divided chorda tympani be stimulated at its distal end, all the former phenomena recur. It may be mentioned, in this connection, though anticipated somewhat, that if the sympathetic plexus surrounding the facial artery be stimulated, the bloodvessels of the glands become very much contracted, the blood flowing more slowly, and darker in color in the veins, and that the saliva then secreted—the so-called sympathetic saliva—is not only diminished in quantity, but contains, in addition to albumen and mucin, sarcode-like bodies. With division of the sympathetic fibres, the secretion of saliva does not altogether cease, a small quantity of the so-called paralytic saliva being secreted, if the tongue be stimulated with induced electricity.

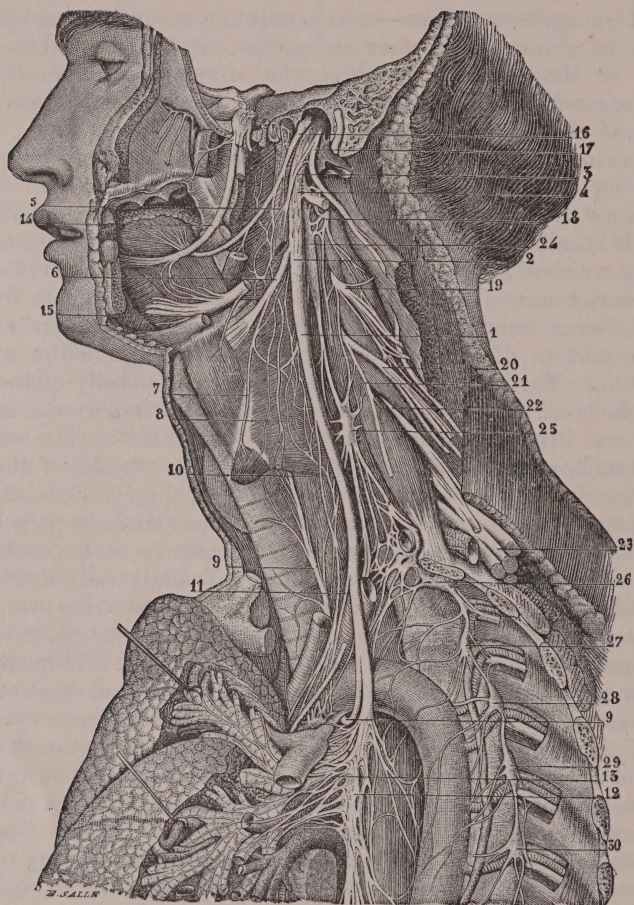
In concluding our account of the functions of the facial nerve it remains for us now briefly to call attention to its external branches. Immediately after the nerve passes out of the stylo-mastoid foramen, as already mentioned, it sends a branch to the glosso-pharyngeal, upon which, as we shall see, the motor properties of the latter nerve depend. The posterior auricular branch receiving sensory filaments from the cervical plexus supplies the attolens and retrahens aurem and the posterior portion of the occipito-frontalis muscle and the adjacent integument. The branches supplying the posterior belly of the digastric, stylo-hyoid and stylo-glossus muscles are important, as these muscles are involved in mastication and deglutition. The temporo-facial branch, as we have seen, supplies all the muscles of the upper part of the face. If this branch be paralyzed, the eye remains, therefore, constantly open through paralysis of the orbicularis palpebrarum muscle, and may become inflamed in consequence from constant exposure. The frontal portion of the occipito-frontalis, attrahens aurem, and the corrugator supercillii are also paralyzed. A striking symptom of paralysis of the facial nerve if these filaments be affected, is inability to corrugate the brow upon one side, as in frowning. Through paralysis of the muscles that dilate the nostrils olfaction and inspiration are also somewhat interfered with. To appreciate the influence exerted by the facial nerve upon inspiration it may be mentioned that in the horse, where the breathing is entirely nasal, death from suffocation very soon takes place if both facial nerves be divided, both nostrils then collapsing and becoming closed with each inspiratory effort.<sup>1</sup> The effect of paralysis of the facial nerve is well seen in cases of facial palsy affecting one side, the distortion of the features being due in such cases to the unopposed action of the muscles upon the unaffected side. When the paralysis is complete the angle of the mouth is drawn to the sound side, the eye on the affected side is widely opened, even during sleep, the lips are paralyzed upon one side, the saliva frequently flowing from the corner of the mouth while the food tends to accumulate between the teeth and cheek through paralysis of the buccinator, mastication in consequence being materially interfered with. If both facial nerves be paralyzed, mastication becomes very difficult, and the face exhibits a peculiarly expressionless appearance.

<sup>1</sup> Bernard: *Leçons sur la physiologie et la pathologie du Systeme Nerveux*, tome ii. p. 308. Paris, 1858.



The next nerve in order, the ninth or glosso-pharyngeal, the consideration of the eighth nerve or auditor being deferred for the present, arises from a column of cells deeply situated beneath the lower and outer part of the floor of the fourth ventricle (Fig. 385, ix), between the auditory and vagal nuclei. From this origin the fibres proceed

FIG. 392.



Distribution of the pneumogastric. 1. Trunk of the left pneumogastric. 2. Ganglion of the trunk. 3. Anastomosis with the spinal accessory. 4. Anastomosis with the sublingual. 5. Pharyngeal branch (the auricular branch is not shown in the figure). 6. Superior laryngeal branch. 7. External laryngeal nerve. 8. Laryngeal plexus. 9, 9. Inferior laryngeal branch. 10. Cervical cardiac branch. 11. Thoracic cardiac branch. 12, 13. Pulmonary branches. 14. Lingual branch of the fifth. 15. Lower portion of the sublingual. 16. Glosso-pharyngeal. 17. Spinal accessory. 18, 19, 20. Spinal nerves. 21. Phrenic nerve. 22, 23. Spinal nerves. 24, 25, 26, 27, 28, 29, 30. Sympathetic ganglia. (HIRSCHFELD.)

forward and outward through the medulla, emerging from the side of the latter by a series of five or six roots containing about 9000 fibres attached to the surface of the restiform body (Fig. 382, viii), the highest being close to the auditory nerve, and passes out of the cranial

cavity through the jugular foramen in company with the pneumogastric and spinal accessory nerves. As the glosso-pharyngeal nerve passes out of the jugular foramen, it expands into the petrous ganglion or ganglion of Andersch from which fine filaments are given off to the pneumogastric and sympathetic nerves. The ganglion gives origin also to the tympanic or Jacobson's nerve; the latter, ascending through the canal of the same name in the petrous portion of the temporal bone, expands upon the promontory of the tympanum into a number of branches which supply the lining membrane of the tympanum, the round and oval windows, and the Eustachian tube. The tympanic nerve gives off also two small branches which pass respectively to the large and small petrosal nerves and filaments to the sympathetic plexus of the internal carotid artery. From the ganglion of Andersch the glosso-pharyngeal nerve descends (Fig. 392) between the jugular vein and the internal carotid artery to the root of the tongue on the inner side of the stylo-pharyngeus muscle terminating in the muscles and mucous membrane of the pharynx, soft palate, tonsils, the root and mucous membrane of the tongue, including the circumvallate papillæ.

During its course the glosso-pharyngeal sends off filaments to the pneumogastric and sympathetic, and, as already mentioned, receives filaments from the facial. That the glosso-pharyngeal nerve is a sensory nerve, at least at its origin, is shown by the loss of sensibility in the parts to which it is distributed and loss of the sense of taste in the posterior third of the tongue following its division in a living animal or paralysis in man, and that stimulation at the root in a living animal fails to produce muscular contractions. Owing, however, to its connections with the facial and with the spinal accessory through the pneumogastric, the glosso-pharyngeal undoubtedly receives motor fibres, to which are due the muscular contractions following irritation of the glosso-pharyngeal when stimulated outside of the cranium, and the difficulty experienced in deglutition, if the nerve be divided in an animal, or be paralyzed in man. It has already been mentioned that the contractions of the muscles involved in deglutition following stimulation of the glosso-pharyngeal are reflex in character, the impressions made upon the latter nerve, like those made upon the palatine branches of the fifth nerve, being transmitted to the medulla and thence reflected through the petrosal nerves to the ganglion of Meckel, and the otic ganglion to the muscles supplied by the latter. The glosso-pharyngeal nerve is therefore sensory in function, endowing the tongue and pharynx with sensibility, and the posterior third of the tongue with the sense of taste, any motor qualities that it may exhibit being attributed to the facial and spinal accessory nerves with which it is connected.

The tenth nerve, the pneumogastric, the par vagum or vagus, arises probably by decussating fibres from a group of nerve cells situated beneath the lowest part of the floor of the fourth ventricle, giving rise to a promontory on the surface of the latter (Fig. 385, X). At the point of the calamus scriptorius, the symmetrically disposed nuclei are in contact at the middle line, but a little higher up are separated by the nuclei, giving origin to the hypoglossal nerves. From this origin the fibres pass forward through the medulla, emerging by twelve or



more roots containing about 9000 fibres attached to the restiform body in a line below those of the glosso-pharyngeal nerve, and leave the cranial cavity, as already mentioned, in company with the glosso-pharyngeal, spinal accessory nerves, and the internal jugular vein. In the jugular foramen (Fig. 392) the pneumogastric nerve presents a well-marked enlargement from one-sixth to one-fourth of an inch in length, the ganglion of the root or the jugular ganglion, from which pass filaments to the facial, and the ganglion of the glosso-pharyngeal and superior cervical ganglion of the sympathetic. After leaving the cranial cavity the pneumogastric nerve presents another enlargement from half an inch to an inch in length, the ganglion of the trunk, from which filaments pass to the hypoglossal nerve and occasionally to the arcade formed by the first two cervical nerves. Immediately after leaving the cranial cavity the pneumogastric nerve receives an important branch from the spinal accessory, and during its course gives off also filaments to the middle and superior cervical and upper dorsal ganglia of the sympathetic, and together with fibres from the glosso-pharyngeal, spinal accessory, and sympathetic forms the pharyngeal plexus. The most important branches given off by the pneumogastric, whose functions we shall study seriatim, are as follows: the auricular, pharyngeal, superior and inferior laryngeal, cervical and thoracic, cardiac, anterior and posterior pulmonary, œsophageal, and abdominal. That the pneumogastric is exclusively sensory at its origin, whatever may be the functions of its branches, appears to be satisfactorily shown, even though indirectly, by experiments like those of Longet<sup>1</sup> made upon horses and dogs just dead, in which stimulation of the nerve at its root failed to produce muscular contractions if the nerve was carefully insulated and all its motor connections divided. That irritation should be followed by muscular contractions if the latter precaution be not observed, should not excite surprise when it is remembered that the pneumogastric receives motor filaments from at least five sources, viz., the facial, spinal accessory, hypoglossal, and first and second cervical nerves, not to speak of the motor fibres derived from the sympathetic. Any muscular contractions ensuing upon irritation of the pneumogastric must therefore be either reflex in character like those of the glosso-pharyngeal already referred to, or be attributed to the stimulation of fibres derived from the motor sources just mentioned.

The auricular or Arnold's nerve, though containing fibres derived from the facial and glosso-pharyngeal nerves, is usually described as being a branch of the pneumogastric nerve, being given off from the ganglion of its trunk. Passing through the temporal bone by the canal of the same name, it is distributed to the external auditory meatus and the membrana tympani, endowing those parts with sensibility. The pharyngeal branches are given off from the superior portion of the ganglion of the trunk of the pneumogastric nerve, but consist largely of filaments derived from the spinal accessory, reinforced, further, during their course, by filaments from the glosso-pharyngeal and superior cervical ganglion of the sympathetic to form the

<sup>1</sup> Physiologie, tome iii. p. 508. Paris, 1869.

pharyngeal plexus, which supplies the muscles and mucous membrane of the pharynx, the motor filaments being derived, as we shall see, from the spinal accessory, and the sensibility being due to the filaments of the pneumogastric proper, and also to those of the pharyngeal branches of the fifth, and of the glosso-pharyngeal. The superior laryngeal nerve arising from the ganglion of the trunk divides into the external and internal branches, the external branch receiving filaments from the inferior laryngeal, and the sympathetic supplies the mucous membrane of the ventricle and crico-thyroid muscles of the larynx, and the inferior constrictor of the pharynx. The internal branch, also receiving filaments from the inferior laryngeal, supplies, like the external branch, the crico-thyroid muscle, and is distributed to the mucous membrane of the epiglottis, the base of the tongue, the aryteno-epiglottidean folds, and the mucous membrane of the larynx as far down as the true vocal membranes. From the anatomical disposition it might be inferred that the general sensibility of the upper part of the larynx and the surrounding mucous membrane, as well as the innervation of the crico-thyroid muscle, was due to the superior laryngeal nerve, and experiment shows that such is the case. Thus, stimulation of the superior laryngeal nerves in a living animal gives rise to intense pain, and causes contraction of the crico-thyroid muscle. It is through the exquisite sensibility of the upper part of the mucous membrane of the larynx that foreign bodies are prevented from entering the air passages; impressions made by such, being transmitted to the medulla, are thence reflected through the inferior laryngeals back to the larynx, bringing about a closure of the glottis. Every one is familiar with the fact that if a crumb of bread, etc., fall upon the aryteno-epiglottidean folds or the edge of the vocal membranes, the sensibility of the parts is such as to excite a convulsive cough, by which the foreign body is dislodged and expelled. The impression conveyed by the superior laryngeal nerve to the medulla being reflected thence through the nerves supplying the expiratory muscles of the chest and abdomen, by which the coughing is accomplished. That this reflex action is due to the sensibility of the laryngeal mucous membrane is shown by the fact that, after division of the superior laryngeal nerve, impressions made upon the mucous membrane fail to bring about such action. The superior laryngeals, also, constitute the afferent nerves in the reflex mechanism by which, through contraction of the constrictors of the pharynx, the act of deglutition is completed. It is interesting to observe that the impressions made upon the mucous membrane of the larynx, and the surrounding membrane, and by which, through reflex action, deglutition is brought about, cause, at the same time, closure of the glottis, and arrest of respiration, thereby protecting the air-passages against the entrance of food or other foreign bodies.

The two inferior or recurrent laryngeal nerves, so called from reascending to the larynx after descending from the pneumogastric, differ slightly in their course on the two sides, that of the left side passing beneath the aorta, that of the right side winding from before backward around the subclavian artery before they ascend in the groove between the trachea



and the œsophagus to the larynx. In other respects, the course and distribution of the two nerves are the same. The curious course taken by the inferior laryngeal nerve, whether of the right or left side, is due to the fact that, while in the embryonic condition, the larynx and heart are in close proximity; through the elongation of the neck, incidental to development, the heart and great bloodvessels recede from the larynx, and, in so doing, drag down with them the inferior laryngeal nerves, which pass, loop-like, around them. It may be mentioned, in this connection, as observed by Owen,<sup>1</sup> and by the author, in four individuals dissected by the latter, that in the giraffe the inferior laryngeal nerves pass directly from the pneumogastric to the larynx, like the superior laryngeals. The significance of this is very evident, for, were the course of the inferior laryngeals in the giraffe the same as in man, the nerve, in descending and ascending through so many feet, would, in all probability, be so stretched and tensed as to render it incapable of performing its functions. As the inferior laryngeal nerves ascend they give off filaments, which join those of the cardiac branches of the pneumogastric, filaments to the muscular tissue, and mucous membrane of the upper part of the œsophagus, to the mucous membrane and inter-cartilaginous muscular tissue of the trachea, to the inferior constrictor of the pharynx, and, as already mentioned, a branch which joins the superior laryngeal, terminating, finally, after penetrating the larynx behind the posterior articulation of the cricoid, with the thyroid cartilage, in all of the intrinsic muscles of the larynx, except the crico-thyroid, which, it will be remembered, is supplied by the superior laryngeal nerve. Direct stimulation of the inferior laryngeal nerves proves what one would be led to expect from their distribution, that they are principally motor in function, and from the fact, as we shall see hereafter, of division of the spinal accessory being followed by loss of voice, the respiratory movements of the glottis being, however, unaffected, but that division of the inferior laryngeal nerves not only involves loss of voice, but paralysis of the respiratory movements of the larynx as well—that their motor filaments are derived at least from two different sources, if not more. To anticipate what we shall see more particularly hereafter, the muscles of the larynx involved in the production of the voice are the arytenoid, the thyro-arytenoid, and the lateral crico-arytenoid, supplied by the inferior laryngeal nerves, and the crico-thyroid, supplied by the superior laryngeal nerves. The posterior crico-arytenoid muscles, supplied by the inferior laryngeal nerves opening the glottis, are, however, respiratory in function. Now, while in an animal the voice is lost after division of the internal branch of the spinal accessories, nevertheless, the glottis, though not closing on irritation, being still capable of dilatation, respiration is not interfered with. Such being the case, if the inferior laryngeal, however, be divided, the glottis is at once mechanically closed with each inspiratory effort, and the animal, if young, dies of suffocation. In adults, however, the cartilages of the larynx being rigid, permit of respiration even after the larynx is paralyzed. The only inference from these facts is

<sup>1</sup> Op. cit., vol. iii, p. 160.

that the fibres of the inferior laryngeal that innervate the muscles of phonation are derived from the spinal accessory, but that those innervating the respiratory movements of the glottis are derived from some other source—from the facial, in all probability, or, possibly, from the hypoglossal, or the cervical nerves that we have seen give off branches to the pneumogastric nerve. Inasmuch, also, as the crico-thyroid muscle is involved in phonation, and as we have seen that the superior laryngeal nerve supplying it receives fibres from the inferior laryngeal, in all probability it is the fibres of the latter nerve that influence the crico-thyroid muscle in phonation, otherwise it is difficult to see why the paralysis of the voice following division of the inferior laryngeal nerve should be so complete. The cervical cardiac branches, two or three in number, arising from the pneumogastric, pass to the cardiac plexus, which consists principally, as we shall see, of fibres derived from the sympathetic. The thoracic cardiac branches given off below the origin of the inferior laryngeal nerves pass, also, to the cardiac plexus.

Contrary to what might have been naturally expected from what we have hitherto learned as to the effect of division and stimulation of nerves, division of the pneumogastric nerve in a living animal, so far from arresting the action of the heart, actually increases the rapidity of its pulsations, while electrical stimulation of the pneumogastric nerve arrests the heart's action in diastole,<sup>1</sup> and causes a fall in the blood pressure. The effect of division of one pneumogastric nerve, however, in a dog or a rabbit, for example, is not by any means as marked as when both nerves have been divided. In the latter case the action of the heart is tremulous, the number of its beats may be doubled, while the respiration, from being momentarily accelerated, becomes calm and profound, but diminished in frequency. That the influence exerted by the fibres of the pneumogastric nerve upon the heart is transmitted centrifugally and is dependent upon its motor fibres is shown by the fact that if the pneumogastric nerve be divided in a living animal and stimulated at its central end none of the effects such as those just described ensue; stimulation of the distal end alone slowing up the action of the heart and causing a fall in blood-pressure; and that if the stimulation be continued too long, so as to exhaust the irritability of the motor fibres, the heart begins to beat again, their inhibitory effect being lost. Further, in animals poisoned with curara, which, as is well known, paralyzes the motor nerves, stimulation of the pneumogastric nerve fails to arrest the action of the heart. That the motor fibres of the pneumogastric nerve influencing the heart's action are derived from the spinal accessory can be shown by experiments like those of Waller,<sup>2</sup> in which after division of the spinal accessory of one side in a living animal, allowing sufficient time to insure disorganization of its fibres, stimulation of the pneumogastric nerve of the corresponding side failed to arrest the action of the heart, the usual effect, however, being observed when the pneumogastric nerve

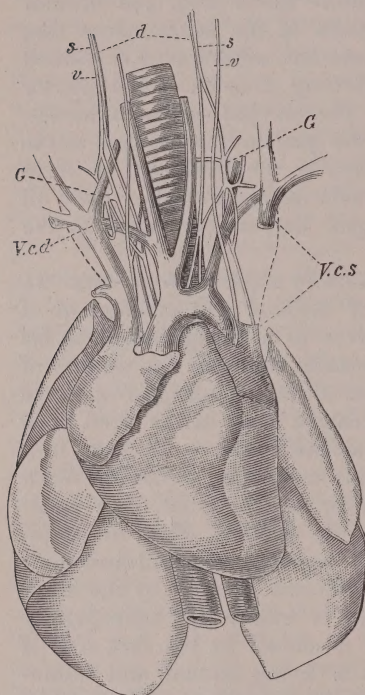
<sup>1</sup> Weber: *Archiv d'Anat. Gén. et de Physiologie*, 1846.

<sup>2</sup> *Gazette Médicale*, 3ième serie, tome xi p. 420. Paris, 1856.



was stimulated on the one side in which the spinal accessory was still intact. That the cardiac branches of the pneumogastric nerves have the same inhibitory influence upon the heart in man as they have been shown experimentally to have in animals, may be inferred from

FIG. 393.



Heart, lungs, and great vessels of the rabbit, with the nerves in relation with them. *V, c, d, V, c, s.* Right and left venæ cavæ superiores; the left vena cava is represented as if cut away, in order to show the nerves. *G.* Ganglion cervicale inferius. *s.* Sympathetic. *v.* Vagus. *d.* Depressor. The dotted lines on each side indicate the position of the phrenic. (LUDWIG.)

FIG. 394.

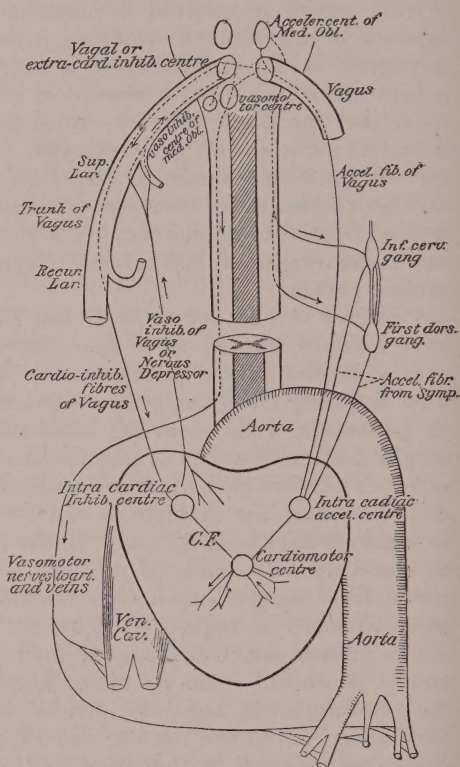


Diagram to aid in understanding the action of the nerves upon the heart. The right half represents the course of the inhibitory, and the left the course of the accelerating nerves of the heart; the arrows showing the direction in which impressions are conveyed. The ellipse at the upper extremity of the vagus looking like the section of the nerve is intended to represent the vagal nucleus or centre. In this diagram the nerves are incorrectly made to cross, instead of passing behind, the aorta.

such pathological<sup>1</sup> cases as those in which the number of heart beats have been known to be reduced to three or four per minute from the compression exerted upon the nerve by pressing upon glands, tumors, etc. That the inhibitory action of the pneumogastric upon the heart can also be exerted in a reflex as well as direct manner, is shown by those cases in which there is a sudden stoppage of the

<sup>1</sup> Muller's Archiv, 1841, Heft 3. Jenaesche Zeits., 165, S. 384.

heart following blows upon the epigastrium, especially after full meals, draughts of cold water, the body being overheated, great emotional excitement, etc., the impression in such cases being transmitted from the general sensory surface to the medulla, and thence reflected through the inhibitory fibres of the pneumogastric to the heart. That the pneumogastric nerve in man contains also special afferent fibres passing from the heart as well as efferent ones to it, by which impressions are transmitted to the medulla, and thence reflected back to the heart by the inhibitory fibres, appears very probable from what has been shown to be experimentally the case in the rabbit and other animals. Thus, if in the rabbit, the so-called depressor<sup>1</sup> nerve (Fig. 393)—that is, the nerve arising partly from the pneumogastric, and partly from the superior laryngeal nerve, be divided, and its distal end stimulated, no effect upon the heart is observed; if, however, the central end of the nerve be stimulated, the action of the heart is arrested, and the blood pressure falls just as if the pneumogastric nerve or the cardio-inhibitory fibres of the same (corresponding in man to the superior cardiac nerve) be stimulated, the action being evidently a reflex one; the impression made upon the central end of the depressor nerve is transmitted to the medulla, and thence reflected back through the cardiac inhibitory fibres of the pneumogastric to the heart. It might naturally be supposed that the inhibitory influence of the cardiac fibres of the pneumogastric is directly exerted upon the heart. That such, however, is not the case, appears from the fact of the latent period—that is, the time elapsing between the application of the stimulus and the inhibitory effect, being very long, nearly one-fifth of a second, instead of one-hundredth of a second, in some cases even two entire beats of the heart intervening before its arrest occurred, indicating that some resistance must be overcome, the inhibitory fibres of the pneumogastric acting upon some mechanism inherent in the heart itself. That such is the case, is shown by the fact that the action of the heart in the eel and the frog can be arrested by direct stimulation, and that in the mollusca, although no pneumogastric nerve is present, the heart can be stopped in diastole<sup>2</sup> by direct irritation. Again, if nicotin or curara be subcutaneously injected in small doses into a living animal the heart beats slower, but on account of the extra cardiac inhibitory centres (Fig. 394) of the pneumogastric becoming soon paralyzed, the heart beats faster; if now muscarin or jaborandi be then administered, the heart will be arrested in diastole, the latter substances appearing to act directly upon intracardiac inhibitory centres. On the other hand, if atropia be injected, then neither muscarin nor jaborandi will have any inhibitory effect upon the heart, atropia appearing to paralyze both the extra- and intracardiac inhibitory centres. Even admitting the existence of extra- and intra-cardio-inhibitory centres, and cardio-motor centres which the intra-cardio-inhibitory centres act upon, such as are hypothetically represented in Fig. 394, it is impossible in the present state of our knowledge to offer any explanation of the inhibitory effect of the pneumogastric nerve upon the heart; it would be useless, there-

<sup>1</sup> Ludwig's Arbeiten, 1866.

<sup>2</sup> Foster: Pflüger's Archiv, Band v. S. 191.



fore, to offer any further reflections upon its functions in this respect, and the same may be said to a great extent of the fall in blood pressure induced through stimulation of the pneumogastric.

The most plausible explanation, and that usually offered, is as follows: A stimulus being applied to the central end of the depressor nerve, the impulse generated, as already mentioned, is not only transmitted to the extra-cardiac inhibitory centres (Fig. 394), whence it is reflected through the cardio-inhibitory fibres of the pneumogastric nerve to the heart, slowing or arresting the latter, but also to a vaso-inhibitory centre, supposed to exist in the medulla, which exerts a restraining or inhibitory influence upon the vasomotor centre of the medulla, the result of which is that the blood pressure sinks through the inhibition of the vasomotor nerve fibres supplying the bloodvessels, and which emanate from this centre. To anticipate a little what will be described more in detail in our consideration of the sympathetic, it may be mentioned, with reference to the explanation just offered of the fall in blood pressure, that, under ordinary circumstances, a nervous influence emanates from the vasomotor centre in the medulla, and which, being transmitted through the spinal cord, spinal and splanchnic nerves, maintains the bloodvessels to which these nerves are distributed in a state of tonic contraction, which keeps up the blood pressure. If, however, the vasomotor centre of the medulla be paralyzed by the action of the vaso-inhibitory centre, induced through the stimulation of the depressor nerve, no such nervous influence being then exerted upon the bloodvessels, the latter dilate, and the blood pressure falls. The result of this is, however, that the medulla receives less blood, so much passing into the abdominal vessels, etc., the consequence of which is, that the extra-cardiac inhibitory centres of the pneumogastric become less active, and the heart resumes its usual activity. That it is to the paralysis of the splanchnic nerve, and consequent dilatation of the great abdominal vessels, that the fall in blood pressure induced by stimulation of the depressor nerve is principally due, is shown by the fact that if the splanchnic nerves be first divided, and then the depressor nerve be stimulated, the blood pressure sinks but little more than when the splanchnics are alone divided. The cardiac fibres of the pneumogastric nerve not only consist of inhibitory or restraining fibres, but also of accelerating ones (Fig. 394). The latter are, however, derived, to a considerable extent, also, from fibres, which, descending from the medulla through the spinal cord, emerge opposite the last cervical and first dorsal ganglia of the sympathetic, which they pass before terminating in the heart. There are good reasons, also, for supposing that just as there are extra- and intra-cardiac inhibitory centres, so there are extra- and intra-cardiac accelerating centres, which act upon the cardiomotor centre just as the inhibitory centres are supposed to do. It may be as appropriately mentioned in this connection, as elsewhere, that while the existence of intra-cardio-inhibitory and accelerating ganglia is hypothetical, an inference from experiments, but not yet demonstrated, that, apart from the small ganglia and nerves, shown by dissection to be distributed through the substance of the heart, there are three well-developed ganglia, which appear to be the centres to which the

efferent nerves convey the impressions made upon the endocardium by the circulating blood, and which transmitted thence through efferent nerves to the muscular fibres of the heart excite the latter to activity. The presence of these ganglia can be readily demonstrated in the heart of the frog, and their functional significance shown by the well-known experiment of Stannius.<sup>1</sup> In the frog, as is well known, the two venæ cavæ unite before entering the right auricle to form a dilatation—the sinus venosus. It is in the wall of the latter, near the opening of the inferior vena cava, that the first of these ganglia, the ganglion of Remak,<sup>2</sup> is situated, the second, or the ganglion of Bidder,<sup>3</sup> being found in the left auriculo-ventricular groove, the third ganglion, or that of Ludwig, in the septum between the auricles. If a ligature be applied between the sinus venosus and the right auricle, the heart stops beating, and remains in a state of diastole.

The sinus venosus, however, continues beating, and the auricles or the ventricle will make a few movements in response to direct stimulation. If now a second ligature be applied between the auricle and ventricle, the ventricle will begin beating again, the auricles, however, still remaining quiet. Many explanations have been offered of the phenomenon just described, one of the simplest and most plausible being that which regards the ganglion of Ludwig as inhibitory in function and exerting greater influence than that of Remak or Bidder, when either of these ganglia is exerted alone. If such be the case, it follows that a ligature being applied to the sinus venosus the inhibitory action of the ganglion of Ludwig being only opposed to the exciting action of that of Bidder, the heart stops, and that after a ligature is applied between the auricles and the ventricle then the inhibitory action of the ganglion of Ludwig being cut off, and there being nothing to counteract the action of the ganglion of Bidder, the ventricle begins to beat again. Whatever the explanation may be of the facts just described, and from what has been said of the cardiac fibres of the pneumogastric nerve, it is evident that the heart possesses an intrinsic nervous mechanism by which, in response to the stimulus exerted by the blood, its fibres are excited to act, and that there exists an extrinsic one by which the action of the heart is inhibited or accelerated.

The pulmonary branches of the pneumogastric nerve are given off as the anterior and posterior branches. The anterior pulmonary branches after sending a few filaments to the trachea, form a plexus which, surrounding the bronchial tubes, is continued to the termination of the latter in the pulmonary air cells. The posterior pulmonary branches, larger and more numerous than the anterior ones, together with fibres derived from the upper three or four thoracic ganglia of the sympathetic, constitute the posterior pulmonary plexus. After giving off fibres to the inferior and posterior portion of the trachea, to the muscular tissue and mucous membrane of the middle portion of the œsophagus, to the posterior and superior portion of the pericardium, the posterior pulmonary plexus surrounds the bronchial tubes, and, like the

<sup>1</sup> Zwei Reihen: Physiologische, Versuche, 1851.

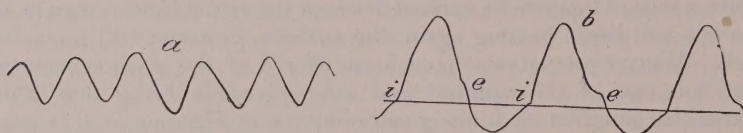
<sup>2</sup> Muller's Archiv, 1844, S. 463.

<sup>3</sup> Archiv f. Anat. u. Phys., 1868, S. 1.



anterior one, is continued with the latter to the air cells. The pulmonary branches of the pneumogastric nerve supply the lower part of the trachea, the bronchi, and the lungs, with both sensory and motor fibres, as shown by experiments like those of Longet,<sup>1</sup> in which, after division of the pneumogastric nerve in the neck, the mucous membrane of the trachea and bronchus became insensible, while stimulation of its branches caused the muscular fibres of the bronchus to contract. It might naturally be supposed, from the pneumogastric nerve giving off the branches we are now considering, to the lungs, that the latter influence in some manner respiration. That such is the case is shown by the fact that after division of the pneumogastrics in a living animal, the division of one nerve having but little effect, that not only is the number of respirations diminished, in some instances being reduced one-half, but that their character is changed, as may be seen from Fig. 395, the

FIG. 395.



a. Tracing of the respiratory movements of the cat. *a* before, *b* after division of both vagi. (CARPENTER.)

respiration becoming much deeper, and that although the same quantity of air is breathed the blood becomes decidedly venous. Death usually takes place after division of the pneumogastrics within from one to six days, occasionally, however, recovery takes place through reunion of the divided ends. In the former case the most marked symptoms are failure of the respiration and increasing sluggishness. After death from division of the pneumogastrics in a mammal, the lungs are found to have become leathery and resisting to the touch, destitute of crepitation, of a dark purple color, sinking when cut up and thrown into water, engorged with blood, and almost empty of air. This peculiar kind of solidification or carnification, as it is called, appears to be due to a traumatic emphysema set up as a consequence of the excessively labored and profound inspirations due to division of the pneumogastrics; the pulmonary capillaries being then ruptured through the distention of the air cells, the blood effused coagulates and so gives rise to the characteristic post-mortem conditions. That this explanation of carnification suggested by Bernard<sup>2</sup> is the correct one, is confirmed by the fact of it not occurring in birds after division of the pneumogastric nerves, since in these animals the lungs are fixed to the walls of the thoracic cavity, and their general relations are such as not to be exposed to great distention in respiration. The only explanation that can be offered of the diminution in the number of respirations, etc., following division of the pneumogastric nerves is that the latter contain fibres, the pulmonary branches, which convey impressions from the lungs, generated through the want

<sup>1</sup> *Traité de Physiologie*, tome iii. p. 535. Paris, 1869.

<sup>2</sup> *Système Nerveux*, tome ii. pp. 353, 368. Paris, 1858.

of air to the medulla, which thence reflected through the phrenic and intercostal nerves, etc., excite inspiratory movements. The want of air being supplied by the filling of the lungs through the inspiratory effort, and the stimulus to the medulla no longer being generated, the passive movements of expiration then ensue. Such being the case, it follows, the pneumogastrics being divided, that the impression due to the want of air is no longer conveyed to the medulla; the respiratory centre of the latter lacking its usual stimulus acts, therefore, less energetically, and the number of respirations diminishes. In a word, the animal not feeling the need of breathing, then inspires much less frequently than ordinary. From what has been said of the function of the inferior laryngeal nerves, it is evident that the pneumogastric nerves being divided in the neck and the laryngeal muscles influencing the vocal cords and the dilatation of the glottis, paralyzed, that the quantity of air entering the lungs will be diminished through the collapse of the glottis. The aëration of the blood being, therefore, very imperfect from this cause as well as from the carnification of the lungs, its venous condition and the general sluggish condition of the system already referred to, is accounted for.

The respiratory centre being, of course, affected in this way is less susceptible to impressions derived from other afferent nerve fibres than those passing from the lungs to the medulla in the pneumogastrics, to be mentioned again presently, and the breathing consequently becoming slower and slower, death finally ensues. That the pneumogastric nerves play an important part in respiration may also be inferred from the respiratory movements being accelerated by the application of a moderate electrical stimulus to the central ends of the divided nerve, no effect following the stimulation of the peripheral ends; the action is evidently, therefore, entirely a reflex one. It should be mentioned, however, in this connection, that the effect of stimulation of the pneumogastric nerves will not only vary according to the strength of the stimulus, but with the state of the breathing. Thus, if the breathing be natural, the effect of a slight stimulus is acceleration of the respiration; if the stimulus be strong, temporary arrest of respiration occurs, and if very strong the diaphragm passes into a tetanic condition. In apnœa, when the blood is overcharged with oxygen, the effect of the stimulus is negative; but if the blood be deficient in oxygen, as in dyspnœa, all the accessory muscles are brought into play and the chest remains in a tetanic condition. From the fact of respiration not ceasing entirely after division of the pneumogastric nerves, but only diminishing in rapidity, and of recovery even taking place after such an operation, it is evident that there must be stimuli by which the respiratory centre of the medulla is called into action other than those emanating in the lungs through the want of air and transmitted by the fibres of the pneumogastric to the medulla. Every one is familiar with the fact that the dashing of cold water in the face, or the first plunge into a cold bath, and the application of a pungent vapor to the nostrils, cause involuntary respiratory efforts. It is well known, also, that the first inspiratory efforts of the newborn child are usually made in response to the stimulation of the cool external air coming in contact with the face, and that



impressions on the general surface, such as a slap on the face or upon the buttocks, will frequently excite the child to breathe when otherwise it would not do so. It would appear, therefore, that impressions made upon the general sensory surface when transmitted to the medulla will cause, through stimulation of the respiratory centre reflexly, inspiratory movements, as well as stimuli in the lungs due to the want of air and transmitted through the pneumogastrics. Finally, there can be little doubt that blood itself when deficient in oxygen acts as a stimulant to the respiratory centre of the medulla, since even after the pneumogastrics are divided if the blood becomes venous in character through artificial respiration being not kept up, the chest of the animal being opened or the blood be cut off from the medulla by opening an artery even though fresh air be supplied to the lungs, in either case violent respiratory movements are made, evidently in response to the stimulus exerted by the non-oxygenated blood upon the respiratory centre of the medulla.<sup>1</sup> The œsophageal branches of the pneumogastric given off both above and below the pulmonary ones unite to form the œsophageal plexus, which supplies the muscular tissue and the mucous membrane of the lower third of the œsophagus. These branches contain both sensory and motor fibres, the latter being probably more numerous, since while the mucous membrane is sensitive to heat and cold, strong irritants, etc., it cannot be said to be acutely sensitive.

That the motor fibres supplying the œsophagus are derived from the pneumogastric nerve can be shown by experiments like those of Bouchardat and Sandras,<sup>2</sup> Chauveau,<sup>3</sup> Longet,<sup>4</sup> Bernard,<sup>5</sup> in which, after division of the pneumogastric nerve in a living animal, the œsophagus was paralyzed and distended by the food vainly endeavored to be swallowed. It is still a question, however, from what nerve the motor fibres of the lower third of the œsophagus are derived, since, according to Chauveau,<sup>6</sup> stimulation of the bulbar roots of the spinal accessory, the most probable source, do not excite contractions of the œsophagus. The abdominal branches of the pneumogastric nerve differ somewhat in their course, according as they are distributed to the two sides. That of the left side, situated anteriorly to the cardiac opening of the stomach, immediately after passing with the œsophagus into the abdominal cavity, gives off numerous branches, some of which are distributed to the muscular walls and mucous membrane of the stomach, while others pass, in company with the sympathetic, along the course of the portal vein to the liver. That of the right side, situated posteriorly, passes through the œsophageal opening of the diaphragm, and, after sending a few filaments to the muscular coat and the mucous membrane of the stomach, is distributed to the liver, spleen, kidneys, suprarenal capsules, and the whole of the small intestine, giving off, also, filaments to the left pneumogastric. If the pneumogastric nerves be divided during full digestion in a living animal in which a gastric fistula has been established, so that the interior of the stomach can be

<sup>1</sup> Flint: *Physiology, Nervous System*, p. 237, 1872.    <sup>2</sup> *Comptes Rendus*, tome xxiv. p. 59. Paris, 1847.

<sup>3</sup> *Journal de la physiologie*, tome v. p. 342. Paris, 1862.

<sup>4</sup> *Traité de Physiologie*, tome iii. p. 547. Paris, 1869.

<sup>5</sup> *Système Nerveux*, tome ii. p. 422. Paris, 1858.    <sup>6</sup> *Op. cit.*, p. 205.

examined, the muscular contractions will be observed<sup>1</sup> to cease instantly, the mucous membrane to become pale and flaccid, the secretion of the gastric juice to be arrested, and the organ to have become insensible. There can be no doubt,<sup>2</sup> also, that stimulation of the pneumogastric nerves causes the stomach to contract, and that digestion may, to a certain extent at least, be reëstablished by stimulation of the peripheral extremities of the divided nerves.<sup>3</sup> Inasmuch, however, as several seconds elapse between the application of the stimulus and the contraction of the stimulus, it is hardly probable, as suggested by Longet, that the muscular contractions of the stomach induced by the stimulation of the pneumogastrics are due to its sympathetic fibres, rather than to the stimulation of the nerve fibres of the pneumogastric proper, the tardiness in action just mentioned being characteristic, as we shall see, of the sympathetic. If such be the case, it would appear that the impressions due to the presence of food in the stomach are transmitted by the abdominal branches of the pneumogastric to the medulla, the efferent impulses being reflected thence to its muscular walls by sympathetic fibres. It must be mentioned, however, that even when both pneumogastric nerves are divided, if the animal survive the operation, in a day or two digestion may be partly reëstablished<sup>4</sup> if the food be finely divided and carefully introduced into the stomach. It is quite possible that the impression due to the presence of food in the stomach and intestines, after reaching the plexus of Meissner, situated in the submucous tissue, and the plexus of Auerbach, lying among the fasciculi of the longitudinal muscular coat, is at once reflected back to their muscular coats without being transmitted to the medulla. Whether the reflex nervous mechanism involved in gastric digestion be such as just mentioned or not, there can be no doubt that digestion in man is very much influenced by the nervous system. Every one is familiar with the fact that digestion may be at once stopped by nervous excitement, such as a piece of bad news, etc.; that there exists an intimate sympathy between the brain and the stomach at all times, and it is difficult to understand by what avenues, other than the abdominal branches of the pneumogastric nerve, impressions are carried to and from these organs. That the abdominal branches of the pneumogastric influence also absorption from the stomach and intestinal digestion may be inferred from the fact that, after division of the pneumogastric nerves, the absorption of poisons is retarded, if not prevented, and that the most powerful cathartics fail to produce their characteristic purgative effects,<sup>5</sup> just as, under similar circumstances, digitalis fails to diminish the action of the heart.<sup>6</sup> Division of the pneumogastric nerve through its abdominal branches produces, also, congestion of the liver, renders the bile watery, and arrests its glycogenic function, the latter being exaggerated by stimulation of the central ends of the divided nerves. The action is a reflex one, as stimulation of the peripheral

<sup>1</sup> Bernard, *op. cit.*, tome ii. p. 422.

<sup>2</sup> Longet, *op. cit.*, tome iii. p. 546.

<sup>3</sup> Tiedemann et Gmelin : *Recherches sur la digestion*, p. 373. Paris, 1827.

<sup>4</sup> Schiff : *Leçons sur la physiologie de la digestion*, tome ii. 389. Florence, 1867. Longet, *op. cit.*, tome iii. p. 549.

<sup>5</sup> Brodie : *Phil. Trans.*, vol. xiv. p. 104. London, 1814. Reid : *Phys. Anat. and Path. Researches*, London, 1848. Wood : *American Journal of the Med. Sciences*, vol. ix. p. 75. Phila., 1870.

<sup>6</sup> Traube : *Gesammelte Beiträge zur Path. u. Physiologie*, Bd. i. S. 190. Berlin.



ends has no effect in this respect, and the efferent impulses are transmitted from the centre, in the medulla, by the sympathetic, probably, and not by the pneumogastric nerve, since division of the latter between the lungs and liver does not affect the production of sugar by the latter.<sup>1</sup>

Resuming what has been said of the functions of the different branches of the pneumogastric nerve, it appears that the auricular branches endow the upper portion of the external auditory meatus and the membrana tympani with sensibility; that the pharyngeal branches supply the muscles of the pharynx with motor filaments derived from the spinal accessory, contributing slightly, also, to the sensibility of the pharynx. To the superior laryngeal branches are due the exquisite sensibility of the upper portion of the larynx, the closing of the glottis against foreign substances, and the production, partly, of the movements of deglutition, and arrest of the diaphragm, the crico-thyroid muscles being also supplied by these nerves. The inferior laryngeal branches, through fibres derived from the spinal accessories, influence phonation, and, through fibres derived from other sources, the respiratory movements of the glottis, while reflexly they cause deglutition and arrest of the diaphragm. The cardiac branches, through fibres derived from the spinal accessories, arrest the action of the heart, and through depressor fibres inhibit the vaso-motor centre of the medulla, and so lower the blood pressure. The pulmonary branches are to a certain extent the avenues by which impressions, due to the want of air, are transmitted to the respiratory centre of the medulla, and thence through reflex action excite inspiratory movements, by which the want of air is supplied. The œsophageal branches supply the lower third of the œsophagus with both motor and sensory fibres, the middle portion being supplied by the posterior pulmonary, and the upper portion by the inferior laryngeal nerves. The abdominal branches influence the production of bile and sugar by the liver, and gastric and intestinal digestion, probably, through conveying impressions from the stomach and intestine, which transmitted to the medulla and thence reflected through the sympathetic, cause secretion.

The spinal accessory or the eleventh nerve (Fig. 381), consisting of from 2000 to 2500 fibres, arises by two distinct sets of roots—upper and lower. The upper root or the bulbar portion, originating in a nucleus lying close to the central canal, and continuous with the nucleus of the pneumogastric nerve (Fig. 385, XI), emerges from the side of the medulla below the latter nerve. The lower roots or the spinal portion, originating in the anterior cornu of the cord, curve backward, and, passing through the gray substance and lateral columns of the cord, emerge from the latter as six or eight filaments between the anterior and posterior roots of the first and seventh cervical nerves inclusive. The spinal accessory nerve so formed enters the cranial cavity by the foramen magnum, and leaves the latter by the jugular foramen in company with the pneumogastric and glosso-pharyngeal, and the jugular vein. During its course the spinal accessory receives

<sup>1</sup> Bernard, *op. cit.*, tome ii. p. 432; *Leçons de physiologie expérimentale*, tome i. p. 324. Berlin, 1855.

from or gives off some filaments to adjacent nerves. Frequently, as it enters the cranial cavity, it receives filaments from the posterior roots of the first two cervical nerves, to which its recurrent sensibility is due; occasionally also it gives off a filament to the superior ganglion or ganglion of the root of the pneumogastric. It also receives filaments from the anterior branches of the second, third, and fourth cervical nerves. After emerging from the jugular foramen the spinal accessory gives off also two branches—internal and external—meriting special notice. The internal branch, consisting principally, if not entirely, of the fibres derived from the medulla, passes to the pneumogastric, subdividing as it joins the latter into two small branches, the first of which constitutes a part of the pharyngeal branch of the pneumogastric as already observed; the second, however, becomes so intimately united with the pneumogastric nerve that its final distribution cannot be made out by dissection alone, experiment only indicating its functional significance, as we shall see presently. The external branch of the spinal accessory, larger than the internal, and derived principally from the fibres of the spinal cord, pass through the posterior portion of the upper third of the sterno-cleido-mastoid muscle, receiving filaments in its course through the muscle from the second and third cervical nerves, to be finally distributed to the trapezius muscle.

That the spinal accessory nerve is essentially motor in function, supplying the muscles just mentioned, can be demonstrated experimentally by cutting through the occipito-atloid ligaments and stimulating the roots of the nerve within the spinal canal by electricity. If, however, the filaments arising from the medulla only be stimulated contractions of the muscles of the larynx and pharynx alone ensue, no movements of the sterno-cleido-mastoid or trapezius being observed. On the other hand, if the filaments arising from the spinal cord only be stimulated then the sterno-cleido-mastoid and trapezius muscles alone contract, the laryngeal and pharyngeal muscles remaining quiescent. Not only does this striking experiment confirm what the distribution of the spinal accessory would lead us to suppose as to its general motor functions, but it also clearly shows that the muscles of the larynx must be supplied by the spinal accessory—that is, that the fibres of the recurrent laryngeal nerves supplying the muscles of the larynx, except the crico-thyroid, are derived not from the pneumogastric but from the spinal accessory nerve.<sup>1</sup> The spinal accessory nerve appears to be endowed also with a certain amount of direct, apart from the recurrent, sensibility already referred to. Whatever sensibility it does possess is, however, due undoubtedly to those filaments derived from the pneumogastric and cervical nerves. In speaking of the functions of the inferior laryngeal branches of the pneumogastric nerve it was mentioned that those nerves consisted of two kinds of fibres, one set influencing the respiratory action of the glottis, another regulating phonation, and that the latter were in reality derived from the internal branch of the spinal accessory. It only remains, therefore, to describe the manner in which this can be demonstrated, since the fibres of the inferior laryngeal

<sup>1</sup> Bernard: *Système Nerveux*, tome ii. p. 296.



nerves influencing phonation cannot be traced by dissection back to the spinal accessory. Bischoff was the first to demonstrate the influence exerted by the internal branch of the spinal accessory nerve upon the production of the voice by opening in a goat the spinal canal through the occipito-atloid space, and dividing all its roots on both sides, the result being entire extinction of the voice, whatever sound was emitted after the experiment being one which in no wise could be called voice.<sup>1</sup> As this method of procedure was however unsuccessful in the six preceding experiments, five of which were performed upon dogs and one upon the goat, even in the hands of such a skilful anatomist and physiologist as Prof. Bischoff, that introduced later and habitually practised by Bernard is a far more satisfactory one. This consists in following by dissection the external or muscular branch of the spinal accessory up to the point where it emerges from the jugular foramen, and where it separates from the internal branch, and then, after seizing the combined trunk between the blades of a forceps, by steady and continuous traction to extract the whole nerve with both its medullary and spinal roots entire; or to remove the medullary portion with the internal branch alone, leaving the spinal portion with the external branch intact, in which case the voice is entirely lost; or to remove the spinal portion with the external branch, leaving the medullary portion with the internal branch intact, in which case the voice is unaffected or in some cases even rendered clearer.<sup>2</sup> It is an interesting fact that in a chimpanzee dissected by Vrolik the internal branch of the spinal accessory was found passing directly to the larynx instead of to the pneumogastric. The usual disposition in this anthropoid appears, however, to be the same as obtains in man, at least such was found<sup>3</sup> to be the case in three individuals dissected by the author. After what has been said of the influence exerted by the pharyngeal branches of the glosso-pharyngeal and of the pharyngeal and inferior laryngeal branches of the pneumogastric in deglutition, and of the inhibitory effects upon the heart by the cardiac fibres of the latter nerve, it is only necessary here to mention again that the motor fibres involved in the performance of the above functions are derived from the internal branch of the spinal accessory, at least partly so in the case of deglutition, and entirely so in that of the inhibition of the heart. As to the function of the external or muscular branch of the spinal accessory, it would appear that its action is to excite contraction of the sterno-cleido-mastoid and trapezius muscles, synchronously with the action exerted by the internal branch upon the laryngeal and pharyngeal muscles, the harmonious action of the muscles so brought about being of advantage under certain circumstances. Thus, in prolonged vocal efforts, as in singing, for example, in which, as which we shall see, the vocal membranes are put on the stretch, the upper portion of the chest is, at the same time, fixed through the action upon the shoulders, to a certain extent at least, of the sterno-cleido-mastoid and trapezius muscles, and in this way the expulsion of

<sup>1</sup> "Qui nentiquam ven appellari potuit." Bischoff: *Nervi Accessorii Willisii Anatomia et Physiologie*, p. 94. Darmstadii, 1832.

<sup>2</sup> Bernard, *op. cit.*, tome ii. p. 296.

<sup>3</sup> *Proc. of Acad. of Nat. Sciences, Philadelphia.*

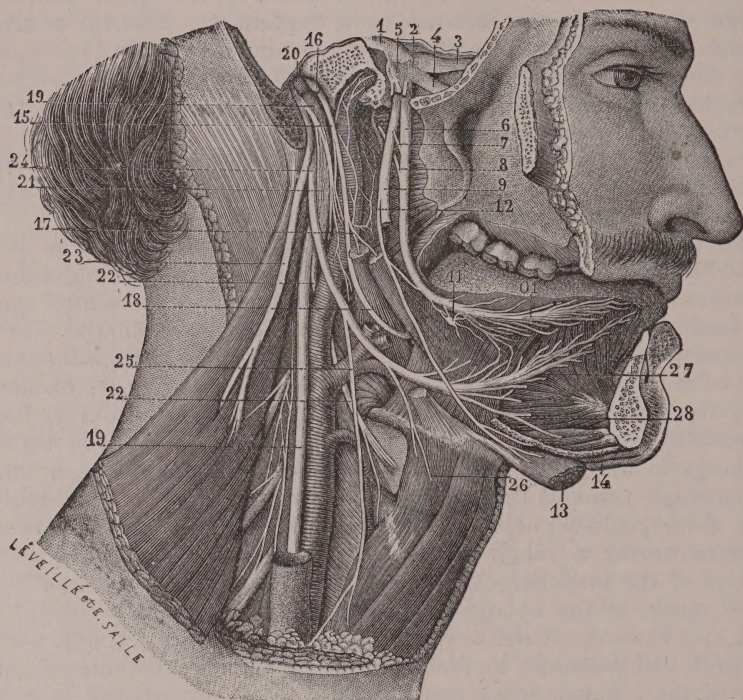
air through the glottis, and upon which the singing depends, can be well regulated. In the same manner, when one makes a muscular effort, the glottis is closed at the same moment that the chest is fixed, respiration being temporarily arrested. The same synchronism in the action of the external and internal branches of the spinal accessory obtain, therefore, in this instance, as in the former. That the external branches of the spinal accessory exert some influence upon the respiratory movement is well seen in animals in which the branches on both sides have been divided, such suffering from shortness of breath after any very great muscular effort, and presenting, also, irregularity in the movements of the anterior extremities, the shortness of breath being apparently due to the want of synchronous action of the sterno-cleido-mastoid and trapezius muscles.

The twelfth nerve, the hypoglossal or sublingual, consisting of from 4500 to 5000 fibres, arises probably by decussating fibres from a long column of nerve cells, the lower part of which lies in front of the central canal on each side, the upper part forming a prominence upon the floor of the fourth ventricle (Fig. 385, xii). Passing thence through the inner part of the olivary body, the fibres emerge as eleven or twelve filaments from the furrow between the anterior pyramid and the olivary body (Fig. 381), which, passing as two distinct bundles through two distinct openings in the dura mater into the anterior condyloid foramen, unite into a single trunk as they emerge from the cranial cavity. Occasionally, the hypoglossal nerve, as it passes through the foramen, receives a filament having a ganglion upon it, arising from the postero-lateral portion of the medulla. This ganglionated filament, or posterior root, so to speak, of the hypoglossal nerve, while exceptionally present in man, is, however, found normally in the dog, cat, rabbit, hog, horse, and calf, and is sensory in function in these animals, the anterior portion of the common trunk corresponding to the hypoglossal in man, being motor. After the hypoglossal passes out of the cranial cavity it gives off (Fig. 396) filaments to the sympathetic, to the pneumogastric, to the upper two cervical nerves, and to the lingual branch of the fifth. Descending behind the pneumogastric nerve it curves downward and forward to the outer side of the latter, between the internal carotid artery and the jugular vein, and penetrates the genio-hyo-glossal muscle, which it supplies, as also the hyo-glossus, lingualis, genio-hyoid, and stylo-glossus muscles. The hypoglossal gives off, also, an important branch, the descendens noni, but which, according to the classification of the nerves usually adopted, would be more correctly called the descending branch of the twelfth, supplying the sterno-thyroid, sterno-hyoid, and omo-hyoid muscles, the thyro-hyoid muscle being supplied by the branch of the same name. From the distribution of the hypoglossal nerve it might naturally be inferred that it is essentially motor in function, any sensibility that it possesses being due to the filaments communicating with the cervical and pneumogastric nerves, and the lingual branch of the fifth. That such is the case is shown by the effect of division of the hypoglossal in a living animal, and of its paralysis in man. Under such circumstances, through paralysis of the tongue, though the tactile and gustatory senses are not affected, masti-



cation is rendered very difficult, if not impossible, while, through paralysis of the muscles depressing the larynx and hyoid bone, deglutition is made difficult; in man the power of articulation is lost as well.

Fig. 396.



Distribution of the sublingual nerve. 1. Root of the fifth nerve. 2. Ganglion of Gasser. 3, 4, 5, 6, 7, 9, 10, 12. Branches and anastomoses of the fifth nerve. 11. Submaxillary ganglion. 13. Anterior belly of the digastric muscle. 14. Section of the mylo-hyoid muscle. 15. Glosso-pharyngeal nerve. 16. Ganglion of Andersch. 17, 18. Branches of the glosso-pharyngeal nerve. 19, 19. Pneumogastric. 20, 21. Ganglia of the pneumogastric. 22, 22. Superior laryngeal branch of the pneumogastric. 23. Spinal accessory nerve. 24. Sublingual nerve. 25. Descendens noni. 26. Thyro-hyoid branch. 27. Terminal branches. 28. Two branches, one to the genio-hyo-glossus, and the other to the genio-hyoid muscle. (SAPPEY.)

This is well seen in cases of glosso-labio-laryngeal paralysis, in which the nuclei of origin in the medulla of the hypoglossal, as well as the facial, spinal accessory, and glosso-pharyngeal nerves are affected by disease, which involves a gradual and progressive paralysis of the tongue, palate, lips, and laryngeal muscles, rendering articulation, and ultimately deglutition, impossible.

In cases of hemiplegia the hypoglossal nerve is usually more or less involved. In such cases the patient protrudes the tongue, the point being deviated to the side affected with the paralysis, owing to the unopposed action of the genio-hyo-glossus muscle of the sound side. That the hypoglossal nerve is a motor nerve—the motor nerve of the tongue, etc.—is further shown by the effect of stimulating the peripheral end of the divided nerve, the tongue, and the muscles to which the nerve is dis-

tributed at once contracting. The hypoglossal nerve, together with the small or motor root of the fifth and the facial nerves, constitutes the efferent fibres by which the reflex action involved in mastication is accomplished, the afferent fibres being the lingual branch of the fifth; and the glosso-pharyngeal nerves, together with the small root of the fifth, facial, pharyngeal, and inferior laryngeal branches of the pneumogastric and cervical plexus, the efferent fibres involved in the performance of deglutition, the afferent fibres being constituted by the palatine branches of the fifth, the pharyngeal branches of the glosso-pharyngeal, the superior laryngeal and œsophagus branches of the pneumogastric.

Having described the distribution and function of the ten pairs of cranio-medullary nerves, and having seen that they arise from gray nuclei in the medulla oblongata, it is evident that the medulla consists, not only as we have seen, of fibres passing from the cord to the ganglion of the base of the brain, but may be regarded, also, as being composed of so many distinct reflex centres, of which the cranio-medullary and spinal nerves constitute the afferent and efferent fibres; the existence in the medulla of about fourteen such centres, probably more, has been established. First. That for closing the eyelids, the afferent fibres being contained in the optic nerve, and the branches of the fifth distributed to the conjunctiva and to the skin of the lids, the efferent fibres in the facial. Second. The centre for sneezing, the afferent fibres, being in the olfactory and the fifth nerve, the efferent in the spinal nerves influencing expiration. Third. The centre for coughing, the afferent fibres rising in the pneumogastric, the efferent being the same as those last mentioned. Fourth. The respiratory centre, or *nœud-vital* of Flourens. Fifth. The masticatory centre. Sixth. The centre of insalivation. Seventh. The centre of deglutition. Eighth. The cardio-inhibitory centres, the afferent and efferent fibres of which have already been referred to. Ninth. The centre for sucking, the afferent fibres of which are in the fifth and glosso-pharyngeal nerves, the efferent the facial supplying the lips. Tenth. The centre influencing the act of vomiting, the afferent fibres being in the pneumogastric, the efferent in the nerves of expiration. Eleventh. The centre of speech—that is, with reference to the movements of the lips, tongue, and larynx. Twelfth. The vaso-motor centre. Thirteenth. The centre inhibiting the reflex centres of the spinal cord.

The medulla oblongata being the seat of the centres receiving the afferent fibres and giving off the efferent ones involved in the performance of mastication, insalivation, deglutition, respiration, circulation, etc., is, therefore, the great coördinating centre of the reflex actions essential to the maintenance of life. Even if all the parts of the brain above the medulla be removed in a living animal, or be undeveloped, as in anencephalous infants, life may yet be maintained by artificial means, since, if food be introduced into the mouth it will be swallowed, the respiratory and circulatory movements will go on in the usual rhythmical manner, the animal or infant will react to impressions made upon the general sensory surface, withdrawing its limbs, etc., if pulled or pinched, may even utter a cry, as if in pain, and yet such an animal or human being cannot be said to be really a sentient, still less an intelligent, being, but merely a nutritive reflex mechanism.



## CHAPTER XLIII.

### THE PONS VAROLII. CRURA CEREBRI. CORPORA STRIATA. THALAMI OPTICI. CORPORA QUADRIGEMINA. CEREBELLUM.

WHETHER reflex action of the spinal cord or medulla be accompanied or not in the lower animals with sensation, volition, consciousness, there can be no doubt that the physical seat of what we call feeling, thinking, etc., in ourselves is situated in some part of the brain above the level of the medulla oblongata, since in the absence of such parts one neither feels, thinks, nor wills. Now, just as we have seen that the spinal cord and medulla consist of nervous centres as well as of fibres passing through them to the ganglia at the base of the brain, so may the pons Varolii or mesencephalon be regarded as consisting, not only of ascending sensory and descending motor fibres connecting the cord with the basal ganglia, and of bridging fibres connecting the lateral lobes of the cerebellum—hence its name—but of gray matter performing the functions of a distinct nervous centre or centres. That the gray matter or tuber annulare (Fig. 397, I) is the essential part of

FIG. 397.



Diagram of human brain in transverse vertical section. 1. Tuber annulare. 2, 2. Crura cerebra. 3, 3. Internal capsule. 4, 4. Corona radiata. 5, 6. Cerebral ganglia. 7. Corpus callosum. (DALTON.)

the pons Varolii is shown by the fact of the bridging fibres of the pons being absent in animals in which the lateral lobes of the cerebellum are undeveloped as in birds. That the tuber annulare, or vesicular matter of the

pons Varolii, is that part of the encephalon in which consciousness first awakens in response to impressions transmitted by the spinal and cranial nerves from the external world appears probable from experiments, such as those of Longet,<sup>1</sup> Vulpian,<sup>2</sup> etc., in which, after removal of the whole encephalon except the pons, medulla, and cerebellum, sensibility to pain still persisted, the cries emitted by an animal so mutilated not being simply reflex in character, such as are heard in an animal possessing only the medulla already referred to, but as really indicating the perception of painful impressions. While it is true that the appreciation of painful and other impressions is not acute, but obscure, nevertheless that such an animal is conscious to a certain extent at least, there can be little doubt, their condition being apparently similar to patients undergoing a severe surgical operation, but imperfectly under the influence of an anæsthetic, and who, while undoubtedly suffering pain at the time, have no recollection of it, the impressions due to the operation not being conveyed to the cerebral hemispheres, and therefore not memorized.

It has already been mentioned that the motor tract beginning in the corpus striatum of one side of the body is continued downward through the anterior or inferior portion of the crus cerebri (crusta) to the decussating fibres of the medulla, and thence to the antero-lateral columns of the opposite side of the cord; that the sensory tract of the cord is prolonged upward through the medulla and posterior or superior portion of the crus cerebri (tegmentum) to terminate in the thalamus opticus of the same side. Such being the case, as might be anticipated if both crura (Fig. 397, 2, 2) are completely divided, sensation and voluntary movement are entirely annihilated throughout the body, division of one of the crura involving paralysis of sensation and motion on the opposite side of the body only. The constant tendency to turn toward the side opposite that of the lesion, the "*evolution du manege*" of Longet, observed when one crus is imperfectly divided appears to be due to the balance of the muscular action being destroyed through the weakening of the sensori motor apparatus of the opposite side. Division of the crus cerebri involves also paralysis of the oculo-motoris of the same side, and partial paralysis of the facial nerve of the opposite side, and is also followed by contraction of the arteries, a rise in blood pressure, and the loss of power to influence voluntarily the action of the sphincter ani, and the constrictor urethræ. In addition to the motor and sensory fibres just referred to, the crura cerebri contain also fibres passing from the gray matter of the medulla and pons to the hemispheres, and of fibres passing forward and backward from the locus niger, or the gray matter separating the crusta from the tegmentum, to the cerebellum, and of fibres passing from the corpora quadrigemina to the cerebellum. The functions of these fibres, so far as known, appear to be commissural in character. If the hemispheres of the brain be removed to the level of the corpus callosum, or the bridge of white substance uniting the cerebral hemispheres, and the latter be divided and turned aside, the lateral ventricles will be exposed—that is, the two cavities

<sup>1</sup> Physiologie, tome iii. p. 396

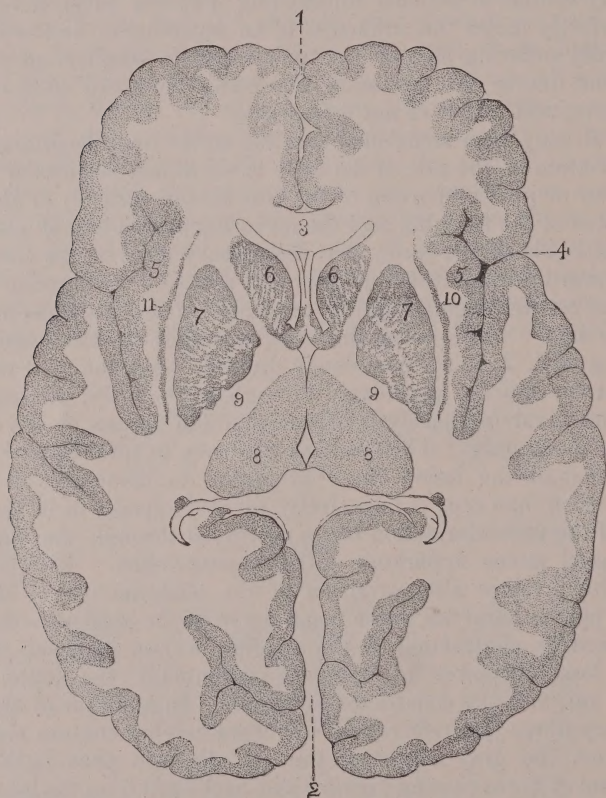
<sup>2</sup> Systeme Nerveux, p. 542. Paris, 1866.



having for their roof the corpus callosum, their floor the fornix, their inner walls the septum lucidum with its enclosed fifth ventricle, their outer walls the corpora striata. Each corpus striatum, so called from presenting a striated appearance on section, projects as a half pyriform prominence into the lateral ventricle, constituting, as just said, its outer wall, the largest anterior portion being known as the head; the narrowest posterior portion the tail, the latter curving backward to the outer side of the thalamus opticus.

Each corpus striatum (Fig. 398) consists of two parts, the intraventricular, or nucleus caudatus (6), and the extraventricular, or nucleus

FIG. 398.



Horizontal section of the hemispheres at the level of the cerebral ganglia. 1. Great longitudinal fissure, between frontal lobes. 2. Great longitudinal fissure, between occipital lobes. 3. Anterior part of corpus callosum. 4. Fissure of Sylvius. 5. Convolutions of the insula. 6. Caudate nucleus of corpus striatum. 7. Lenticular nucleus of corpus striatum. 8. Optic thalamus. 9. Internal capsule. 10. External capsule. 11. Claustrum. (DALTON)

lenticularis (7), the two being separated by the internal capsule (9), or the diverging fibres of the crus cerebri, to which the corpus striatum owes its name, the external capsule (10) with the claustrum (11) lying to the outer side of the nucleus lenticularis and close to the insula or

island of Reil (5). While it is quite possible that some of the divergent fibres of the crus cerebri pass directly through the corpus striatum to the gray matter of the convolutions of the hemispheres, it appears more probable that the corona radiata (Fig. 397, 4), or the cone of fibres radiating out to the convolutions, originate *de nova* in the corpus striatum, and are not merely continuations of the internal capsule. If now the fornix or floor of the lateral ventricle be removed, a narrow triangular cavity will be exposed, the third ventricle, communicating, on the one hand, with the lateral ventricles by the foramina of Monro, and on the other with the fourth ventricle by the iter, the latter passing under the corpora quadrigemina, to be mentioned presently. The floor of the third ventricle is formed from before backward by the optic commissure, infundibulum, mammillary eminences, posterior perforated space, and cerebral crura; its walls, by the thalami optici, situated on the inner side of the crura cerebri, and separated from the corpora striata by the internal capsule and tænia semicircularis. The more prominent portions of the thalamus opticus anteriorly and posteriorly are known as its tubercles; beneath the posterior ones are situated the corpora geniculata, giving partial origin to the optic tracts. Each thalamus opticus consists internally of white matter, externally of both white and gray matter, and is connected, like the corpus striatum, with the convolutions of the hemispheres by diverging fibres. It will be observed from this brief sketch of the structure and relation of the corpora striata and thalami optici to the crura cerebri on the one hand, and the cerebral convolutions on the other, that there are three distinct sets of nerve centres, and three distinct sets of nerve fibres through which the impressions from the periphery are transmitted to the convolutions of the hemispheres and in the reverse direction, viz., nerve centres, first, the gray matter of the cord, second, the basal ganglia, and third, the gray matter of the convolutions of the hemispheres; nerve fibres, first, the fibres of the nerves connecting the periphery with the gray matter of the cord, second, the fibres of the gray matter and of the columns of the cord connecting the gray matter of the cord with the basal ganglia, and third, the fibres of the corona radiata connecting the basal ganglia with the gray matter of the convolutions of the hemispheres. Such being the case, if what we have called the motor and sensory tracts of the spinal cord in man have the functional significance attributed to them, and if the corpus striatum is the beginning of the motor, and the thalamus opticus the ending of the sensory tract, it is difficult to avoid drawing the conclusion that these ganglia are respectively motor and sensory in function. One of the best established facts in human or animal cerebral pathology is that a destructive lesion of the corpus striatum, whether produced by disease or experimentally, is followed by a paralysis of motion of the opposite side of the body, sensation remaining unimpaired. It is true that in some exceptional cases the paralysis is on the same side of the body, but there is no question in such cases as to the paralysis due to the lesion of the corpus striatum being that of motion. Of this there can be no doubt. Apart from the number of cases that have been recorded, the author has had ample opportunities afforded, both in man and animals, of satisfying himself as to this point. It has also been shown by



several experimenters<sup>1</sup> that electrical stimulation of the corpus striatum in a living animal, monkeys, dogs, cats, etc., causes a general unilateral contraction of the muscles of the opposite side of the body, the latter being thrown into a condition of pleurosthotonus, in which it is bent to the opposite side, the flexor muscles being contracted apparently more than the extensor ones. It is well known also, that in the cetacea, the whale, dolphin, the elephant, etc., very muscular animals, the corpora striata are not only absolutely but relatively large and well developed. The facts of pathology, experiment, and comparative anatomy, confirm, therefore, the view based upon their anatomy, that the function of the corpora striata is essentially motor. While lesions of the thalamus opticus are not of infrequent occurrence in man, from the fact that the corpus striatum and adjacent parts of the hemispheres are usually involved, conclusions as to the functions of these ganglia, based upon the loss of sensibility, etc., following their destruction, cannot be accepted with the same confidence as in the case of the corpora striata. Nevertheless, if the lesion be limited, as is sometimes the case, to the corpus striatum and the thalamus opticus, and the destruction of these two ganglia is followed by loss of motion and of sensibility on the opposite side of the body, and if it be admitted that the function of the corpus striatum is motor, the conclusion that the thalamus opticus is sensory in function becomes then unavoidable. Indeed, it could not be otherwise, since after destruction of the thalamus opticus no other avenue is left by which sensory impressions can be transmitted from the general periphery of the body to the cerebral hemispheres. That the thalamus opticus is essentially sensory in function is further shown by the fact of its destruction in man being followed by loss of general and special sensibility on the opposite side of the body, tactile sensation being impaired, and hearing and vision in some cases affected.<sup>2</sup>

The results of experiments performed upon animals are unfortunately so contradictory and unsatisfactory that they throw little or no light upon the functions of the optic thalami in them and still less in man. It appears, however, to have been established by the fact of electrical stimulation failing to produce muscular contractions that the thalamus opticus has not motor significance, confirming what has just been said as to its having sensory functions. While it must be admitted that the evidence adduced in favor of the thalamus opticus being sensory is not as conclusive as that in favor of the corpus striatum being motor in function, nevertheless what positive evidence there is bearing upon this subject favors such a view while the negative evidence is not against it. That the paralysis of motion and sensation following lesions of the corpora striata and thalami optici is not due simply to the motor and sensory impulses being normally transmitted through these ganglia from or to the convolutions of the hemispheres, and that after the destruction of these ganglia no avenues are left for the transmission of such impulses, is shown by the fact that after removal of the cerebral convolutions in a

<sup>1</sup> Ferrier: *The Functions of the Brain*, p. 237. New York, 1876. Burdon Sanderson: *Centralblatt*, p. 513, 1874.

<sup>2</sup> Ley's *Recherches sur le Systeme Nerveux*, 1865, p. 538. Crichton Browne: *West Riding Asylum Reports*, vol. v. p. 227, 1876. Ferrier, *op. cit.*, p. 239.

mammal the power of movement and sensation remains. Thus, for example, in a rabbit the cerebral hemispheres having been removed, while there is nothing observed to indicate that its sensations ever give rise to ideas—that is, that it perceives—nevertheless, it feels even it does not think; it sees, hears; if pinched, it cries; when stirred up, it runs or leaps forward, avoiding with more or less success obstacles placed in its path. The animal has undoubtedly possession of its senses, can execute all its bodily movements, but its intelligence appears to be gone, at least objects which would have ordinarily pleased or terrified it make no impression whatever upon it. It must be borne in mind, however, that in any application to be made of such results with the view of elucidating the functions of the basal ganglia in man, that it does not necessarily follow that a human being, or even a dog deprived of its cerebral hemispheres, should be in exactly the same mental condition as a rabbit under similar circumstances. On the contrary, there is good reason for supposing that as we pass from the lower to the higher mammals the seat of voluntary motion and sensation is removed to higher and higher levels in the encephalon; the cerebral convolutions being more important in this respect in man than in a dog, and the basal ganglia more important in the dog than in the rabbit, and so on. The most marked contrast in this respect is presented by fishes, in which the corpora striata are relatively well developed, the cerebral hemispheres but little so—in fact, the latter are only represented, more particularly in the cartilaginous fishes, by the thin film of nervous matter covering in the cavity or ventricle, of which the corpora striata constitute the floor; the so-called optic lobes in fishes represent, probably also not only the optic lobes of the higher vertebrates, but also the thalami optici as well. Undoubtedly a rabbit can do more without its basal ganglia and cerebral convolutions than a dog, and a dog with its basal ganglia but without its hemispheres than a man without the latter. It becomes, therefore, a very difficult matter to say just where sensation begins in man, and still more, where sensation is accompanied or gives rise to ideation and volition. If it be admitted, however, that even after removal of all the encephalon above the pons, feeling even if obscure persists it might be expected that sensation would be more defined, more acute, if higher ganglia such as the thalami optici remain intact. While it cannot be said then that the functions of the basal ganglia have been established beyond doubt, in all probability the thalamus opticus is the ganglion of general sensibility, the corpus striatum of motion, and in the lower mammals of voluntary motion very probably. Even if such, however, be not exactly the case, and it be supposed that an impression made upon the periphery must be transmitted to the cerebral convolutions to be thoroughly appreciated, and that a voluntary impulse developed in response to such a sensation must emanate in the same, the connections of the basal ganglia through the corona radiata, with the convolutions of the hemispheres, and with each other, offer an avenue for the performance of reflex actions already referred to, which originally being accompanied with both sensation and volition, in time come to be performed without either. For with the constant repetition of a particular action involving sensation and volition, it is natural to



suppose that the circuit traversed might become shorter and shorter, and that impressions which originally reached the cerebral hemisphere before being reflected back, simply passing through the basal ganglia to and fro, gradually take a shorter course, and reaching the thalamus opticus are at once reflected back through the corpus striatum, short-circuited, so to speak.

Such a change would obviously be of advantage to the economy, since the basal ganglia, taking upon themselves, so to speak, the performance of the work done formerly by the hemispheres, more opportunity would be afforded the latter of doing intellectual work. It has already been mentioned that the iter or way by which the third and fourth ventricles communicate with each other, passes underneath the corpora quadrigemina. The latter consist of a white quadrate mass more or less divided upon its upper surface by a crucial depression into four eminences, the so-called nates and testes, optic lobes, or quadrigeminal bodies, whence their name. The corpora quadrigemina, or the optic lobes, as we shall hereafter for brevity designate them, are attached laterally to the thalami optici between which they are situated, and also to the geniculate bodies, and therefore indirectly with the

FIG. 399.

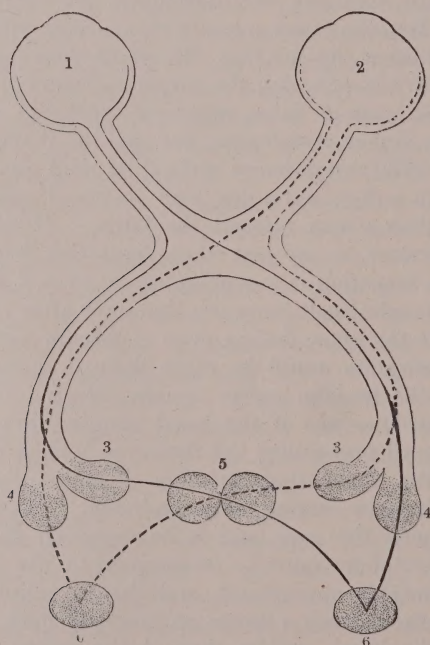


Diagram of the optic nerves and tracts, in man. 1. Left eyeball. 2. Right eyeball. 3, 3. Corpora geniculata interna. 4, 4. Corpora geniculata externa. 5. Tubercula quadrigemina. 6, 6. Centres of vision in the cerebral hemispheres. (DALTON.)

optic tracts, and inferiorly through the superior penduncles of the cerebellum, between and attached to which is the valve of Vieussens, to the

cerebellum, and also through the fibres descending through the pons and embracing the olivary body to the motor columns of the cord. Such being the anatomical disposition of the optic lobes, it might be surmised that with their destruction sight would be abolished and muscular action affected, which is found to be the case in those instances where the optic lobe has been destroyed by disease in man, or by experiment in animals. Further, on the supposition that there is a total decussation of the optic tracts, and, according to the view entertained by Charcot (Fig. 399), it becomes intelligible, not only why destruction of the optic lobe of one side entails the total loss of sight in the opposite eye, but through the connections of the optic lobe with the thalamus opticus and adjacent fibres of the corona radiata why lesions situated in that part of the brain should be accompanied by impairment of sensibility as well as loss of vision. The optic lobe, as might be expected, constitutes also an important part of the reflex mechanism by which the coördination of the eyeballs and the contraction of the pupil are effected, the optic nerve being the afferent nerve and the oculomotorius the efferent nerve, the reflex centres being situated either in the optic lobe or immediately beneath it. Apart from the anatomical fact that the optic lobes are connected with the motor tracts of the spinal cord, which would, as already remarked, indicate that these ganglia influence muscular action in some way, it is well known that the optic lobes are not invariably developed in proportion to the eyes, but, on the contrary, may be quite large, though the eyes and optic tracts be but small, little developed, or even wanting altogether, as, for example, in the myxine or hag fish, and the *aplerechthys cæcus* among fishes, in the *proteus* and *cecilia* among batrachians, and in moles and shrews among mammals, which show that the optic lobes have other functions beside those influencing vision. Now, while the experience of the author has been like that of other experimenters, that destruction of the optic lobes involves, in addition to loss of sight, disorders of equilibrium and want of muscular coördination, nevertheless, it must be mentioned that a very great difference prevails in this respect according to whether the animal upon which the experiment of removing the optic lobe is performed be a batrachian, bird, or mammal, the optic lobes relatively to the cerebral hemispheres being so much better developed in the lower than in the higher vertebrates. Thus, for example, a frog with its optic lobes intact, but without its cerebral hemispheres, can coördinate its muscles for the performance of ordinary actions better than a pigeon or a rabbit similarly conditioned, and the latter better than a monkey or man. It may be mentioned also, in this connection, that the want of coördinating power, etc., following destruction of the optic lobes is not due, as might be supposed, to the blindness entailed, since in the frog, for example, if the eyes be destroyed but the optic lobes be left intact, such disorders as those ensuing upon the destruction of these ganglia are not observed. It is well known that if all the encephalic centres above the optic lobes be removed in the frog, gentle stroking of the back excites the animal to croak. The croaking entirely ceasing, however, if the optic lobes be removed, the natural inference is that these ganglia contain the reflex centres through which the croaking is produced. As



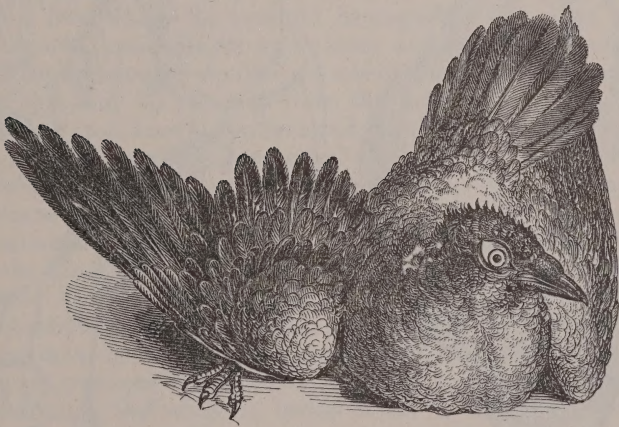
certain plaintive cries emitted by the rabbits cease after removal of the optic lobes, it is possible that a similar reflex centre exists in the optic lobes of mammals as well as in those of frogs.

Taking this latter fact into consideration, together with that of the circulation and respiration being modified by electrical stimulation of the optic lobes, the blood pressure being increased, the heart slowed, the respiration deepened exactly in the same manner as when the sensory nerves are powerfully excited, and that contractions of the stomach, intestines, and bladder also follow, it would appear that the optic lobes are also concerned in the reflex manifestation of motion, as well as of influencing muscular coördination and vision. While there can be no doubt that destruction of the optic lobes in man and animal entails loss of vision and impairs the power of muscular coördination, it still remains to be determined whether these effects are due simply to the fact that the fibres by which impressions made upon the retina and periphery reach the visual and coördinating centres pass through the optic lobes, or whether these ganglia are themselves the seat of the visual and coördinating centres. That the latter is not the case in the higher vertebrates, whatever it may be in the lower ones, is shown by the fact that destruction of the angular convolution, or gyrus, in a mammal, the monkey, for example, entails loss of vision as certainly as destruction of the optic lobe itself; on the other hand, it cannot be denied that even after destruction of the angular gyrus in a mammal, or entire removal of the cerebral hemispheres in a bird, the mere sensation of sight persists—that is to say, the impression of light upon the retina still gives rise to the mere sensation of sight, but that the sensation no longer gives rise to such ideas as are usually developed in response to the stimulus of light—that is to say, the animal with its optic lobes intact, but with its cerebral hemispheres removed, may see, but does not think. It is not impossible, however, that in the lower vertebrates the true visual and simply sensory centres may be located together in the same part of the encephalon, the mass, for example, representing in fishes the optic lobe and thalamus opticus, containing also the representative of the angular gyrus of the higher vertebrates. The relation of the optic lobes to the true coördinating centre located, in all probability, at least in birds and mammals in the cerebellum, can be more conveniently discussed after the functions of the latter organ have been considered. It may be mentioned, however, in this connection that, after removal of both the cerebral hemispheres and cerebellum in the frog, the optic lobes being still intact, the power of muscular coördination remains unaffected, proving that in such animals at least the centre of muscular coördination is not located in either of those portions of the encephalon, whatever may be the case in higher vertebrates.

It has already been mentioned incidentally that the optic lobes are connected posteriorly with the cerebellum through the superior peduncles of the latter. The fibres of the superior peduncles passing forward and upward to the testes ascend through the crura cerebri to the thalamus opticus and corona radiata, some of the fibres decussating beneath the optic lobes. Inferiorly the superior peduncles are connected with the vermiform process of the cerebellum and with the corpus dentatum,

or pouch-like layer of gray matter within the white matter of the lateral hemispheres. The cerebellum, constituting about one-eighth of the bulk of the brain, and situated in the posterior fossæ of the cranial cavity, consists of two lateral portions, the hemispheres, the anterior rounded eminences of which are known as the amygdalæ, or the tonsils. The hemispheres, though separated behind and below by a wide deep groove, the vallecule or valley, are connected by an intermediate worm-like ridge, the vermiform process, the portion of the latter situated between the tonsils being called the uvula, while just above the tonsils, and separated from them by a fissure, may be seen the flocculi, or pneumogastric lobules, so called from their vicinity to the nerve of the same name. Each lateral hemisphere and vermiform process essentially consists internally of a prismoid trunk of white substance, from which emanate about a dozen broad thin laminæ; the latter subdividing again into secondary thinner laminæ, and the gray substance enfolding them, gives rise to the convolutions and fissures observable on the surface of the organ. The middle peduncles of the cerebellum constituting, as already mentioned, the transverse commissural fibres of the pons Varolii connect the two lateral hemispheres, while the inferior peduncles pass downward into the restiform bodies of the medulla, and are connected with the spinal cord. If the cerebellum be removed in a bird, a pigeon, for example (Fig. 400), though the animal still feels, thinks, wills, it is

FIG. 400.



Pigeon, after removal of the cerebellum. (DALTON.)

unable to stand or fly. If placed upon the back, it is unable to rise. If food be placed within its reach, though it sees it, it cannot pick up the food. Instead of remaining quiet, it is in a continual state of restlessness and agitation. In a word, though able to make voluntary movements, the animal has lost the power of coördinating its movements for the performance of a definite object, or of maintaining its equilibrium. Its movements highly resemble those of a drunken man. Essentially the same results are obtained if the cerebellum be removed in a mammal. Undoubtedly, then, very remarkable disorders, both as regards the main-



tenance of equilibrium and power of locomotion ensue upon destruction of the cerebellum in mammals and birds, although, as already mentioned, no perceptible change is observable in these respects in the case of frogs, in which the cerebellum has been removed.

Differences of opinion still prevail among pathologists as to whether lesions of the cerebellum in man give rise to the same disorders as observed in mammals and birds, in which the cerebellum has been removed, and even though it be admitted that entire absence of the cerebellum, as shown by post-mortem examinations, was not accompanied during life with loss of the power of locomotion, or of the maintenance of equilibrium, nevertheless it may be questioned whether there is a well authenticated case in which locomotion and equilibrium remained unaffected, extensive lesions of the cerebellum existing. Such cases as where there was a congenital absence of the cerebellum, unaccompanied with any disorders of locomotion, etc., being explainable on the supposition that, as in the case of the frog, the function of the cerebellum was performed by other ganglia, probably the optic lobes. On the supposition that the cerebellum is the centre for the maintenance of equilibrium and of muscular coördination, it ought to be best developed

FIG. 401.

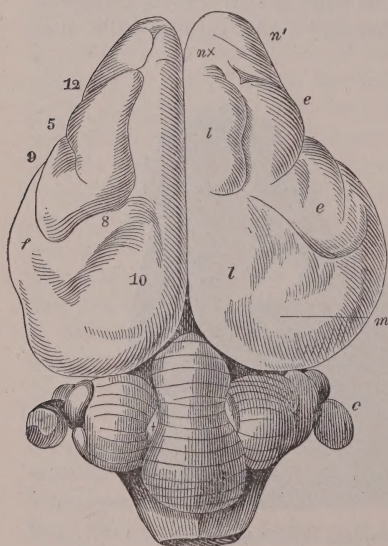
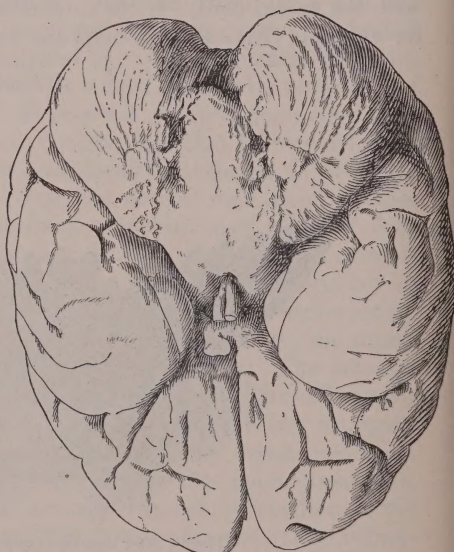
Brain of kangaroo, *macropus major*. (OWEN)

FIG. 402.



Brain of chimpanzee.

in those animals which exhibit such powers in a marked degree, and such we find to be the case. Thus in the shark, for example, in which, of all fish, the muscular system is best developed, and the power of coördination so perfect, as shown, for example, in the manner in which it throws itself upon its back at the instant of seizing its prey; the mouth being situated beneath, and posteriorly, the cerebellum is larger and more complex in its structure than in any other fish. Among birds, also, the cerebellum is particularly well developed in the carnivorous

raptures, in which muscular actions, such as are involved in the swooping down by them upon prey from immense heights, require very nice adjustment of coördination. Among mammals the cerebellum is large; in the kangaroo (Fig. 401), whose peculiar mode of progression necessitates considerable muscular coördination, while, in the elephant, in which great muscular coördination is demanded, owing to the enormous muscular development, and in the case of the posterior extremities to the absence of the round ligament of the hip-joint, the cerebellum is very large, being equal to one of the hemispheres. In the anthropoid apes, also, which not unfrequently assume the semi-erect attitude, the cerebellum is larger than in the remaining monkeys. Indeed, in the chimpanzees (Fig. 402) and oranges dissected by the author<sup>1</sup> the cerebellum was found so well developed as to extend slightly beyond the posterior lobes of the cerebrum, which is not the case in monkeys generally, in the baboons, macacques, spider-monkeys, etc., the cerebellum being perfectly covered by the posterior lobes of the cerebrum, as in man. That the cerebellum, at least in mammals, birds, and fishes, is the centre for the maintenance of equilibrium and muscular coördination is not only shown by experiment, pathology, and comparative anatomy, but from the fact of the tactile, visual, labyrinthine, and perhaps visceral impressions upon which the maintenance of equilibrium and muscular coördination depend, being transmitted from the periphery through nerves which directly or indirectly terminate in the cerebellum, as we shall now endeavor to show. It has already been mentioned that a frog from which the cerebral hemispheres have been removed, but which still preserves its optic lobes and cerebellum, retains the power of maintaining its equilibrium and of muscular coördination. If, however, the skin be removed from the hinder legs of such a frog, the animal at once loses this power and falls like a log if the position of its support be changed, the removal of the skin making impossible the transmission of those afferent tactile impressions which through some reflex centre give rise to those efferent muscular actions requisite for the maintenance of equilibrium. That this reflex centre is situated in man in the cerebellum, and that these afferent tactile impressions are transmitted by the posterior columns of the spinal cord, is rendered very probable from the fact that sclerosis of these columns causes locomotor ataxia, a disease specially characterized not by a loss of sensibility but of power of coördination, and that the posterior columns of the cord through the restiform bodies of the medulla terminate in the cerebellum. While visual are not as important as either tactile or labyrinthine impressions in the maintenance of equilibrium, since the latter almost suffice in the absence of the former, nevertheless they exercise a certain amount of influence. Thus, in cases of locomotor ataxia, for example, equilibrium and coördination are not altogether impossible, even though the tactile impressions be wanting, so long as the labyrinthine and visual impressions persist, and in such cases when the transmission of tactile and labyrinthine impressions are perfect, the absence of visual ones always entails some slight want in the coördi-

<sup>1</sup> Proc. Acad. of Nat. Sciences, 1879.



nating power. That such visual impressions are transmitted to the cerebellum, is rendered very probable when it is remembered that the optic lobes are connected with the cerebellum both through the superior peduncles and valve of Vieussens. As is well known, remarkable disturbances of equilibrium ensue, if the membranous semicircular canals of the internal ear be divided in a bird or mammal, or if they are diseased as in Ménière's disease in man, which vary according to the seat of the lesion. Thus, if the horizontal canals be divided in a pigeon, for example, rapid movements of the head in a horizontal plane, from side to side, follow, with oscillation of the eyeballs, and a tendency to spin around on a vertical axis is manifested.

If, however, the posterior or inferior vertical canals be divided, the head is moved rapidly backward and forward, and the animal tends to turn somersaults backward head over heels, whereas if the superior vertical canals be divided, the head is moved rapidly forward and backward, and the animal tends to make forward somersaults heels over head. It would appear from the researches of Goltz,<sup>1</sup> Mach,<sup>2</sup> Brewer,<sup>3</sup> and Crum Brown<sup>4</sup> among others, that the character of the impressions made upon the vestibular nerves depends upon the degree and relative variations in the pressure exerted by the endolymph upon the ampullæ of the membranous canals, to which, as we shall see hereafter, these nerves are distributed. Such being the case, it is obvious that if the semicircular canals be divided disturbances of equilibrium must ensue, the natural tension of the endolymph being thereby altered, which will vary according to the particular semicircular canal affected. It may be mentioned in this connection, that pigeons in which the semicircular canals have been divided on one side in time regain the power of maintaining their equilibrium, but if the canals be divided on both sides, they never again are able to assume their natural position, the most strange and bizarre attitudes being taken. Whatever may be the nature and mechanism of the labyrinthine impressions, there can be no doubt as to the influence exerted by them in the maintenance of equilibrium, since in their absence the same becomes impossible even though the tactile and visual impressions persist. That the membranous semicircular canals and the auditory nerve together constitute an afferent system by which impressions are transmitted to the cerebellum, acting as a reflex coördinating centre, appears highly probable when it is remembered that division of the auditory nerve entails disturbances of equilibrium, that the auditory nerve through the restiform bodies is directly connected with the cerebellum, and that a great similarity exists between the effects of destruction of the cerebellum and division of the semicircular canals. Thus, destruction of the anterior portion of the middle lobe of the cerebellum, like that of the superior vertical canal, involves displacement of equilibrium forward around a horizontal axis, destruction of the posterior part of the median lobe like that of the posterior vertical canal, displacement backward around a horizontal axis, destruction of the lateral lobes of the cerebellum, like that of the

<sup>1</sup> Pflüger's Archiv, 1870.

<sup>2</sup> Med. Jahrbucher, Heft i., 1874.

<sup>3</sup> Sitz. u. der K. Acad. der Wiss., Wien, 1873.

<sup>4</sup> Journal of Anat. and Phys., May, 1874.

horizontal canals, lateral displacement around a vertical axis. The cerebellum appears, therefore, to be the reflex centre by which the afferent impressions transmitted by the cutaneous, optic, and acoustic nerves are coördinated with the efferent ones for the maintenance of equilibrium and locomotion. That such reflex actions are accompanied now, or originally at least, with consciousness, and that the cerebellum is that part of the encephalon in which the ideas of space are developed, is rendered very probable when it is remembered that many actions involving muscular coördination, which are performed now unconsciously, were originally accompanied by both sensation and volition, and that the disorders of equilibrium and locomotion following destruction of the cerebellum or of the afferent system leading to it, imply a perversion in the ideas of space relations.

In concluding our account of the cerebellum it should be remembered that as its lateral peduncles decussate in the pons Varoli the cerebellum is connected with the motor tracts of the opposite side of the cord, but as the latter decussate in the medulla, the lateral lobes of the cerebellum in this way influence the muscles of the same side of the body.



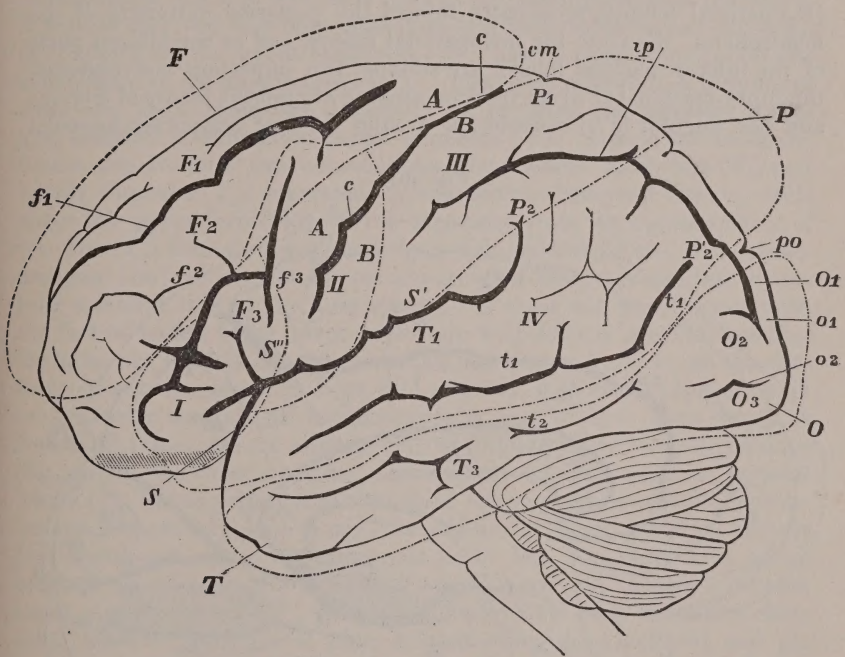
## CHAPTER XLIV.

### THE CEREBRAL HEMISPHERES.

THE cerebral hemispheres, so called on account of their hemispherical form, are two ovoidal masses flattened at their mesial surface, where they are separated by the great longitudinal fissure. They consist of gray or vascular and of white or fibrous nervous tissue. The gray substance, like that of the cerebellum but unlike that of the spinal cord, situated externally and varying between two and three millimetres in thickness, sinks at intervals into the white substance to a depth of from ten to twenty-five millimetres, invaginating itself—that is, folds inward to return upon itself again, and so gives rise to the convoluted and fissured surface so characteristic of the brain of man and of many mammals. It is evident that through this convoluted arrangement the hemispheres contain far more gray matter than if they were smooth, on the same principle that a pocket handkerchief occupies much less room when folded up than when laid out smooth, and that the deeper and more numerous the fissures the greater the amount of gray matter present. The gray matter of the convolution or cortical layer of the hemispheres, consisting of a granular matrix in which are imbedded nerve-cells, connected through their prolongations with the nerve fibres of the white substance, is composed of six or more layers distinguished by the character of the nerve cells they contain. Of the latter may be mentioned the so-called pyramidal cells, varying between 10 micro-millimetres and 40 micro-millimetres ( $\frac{1}{2500}$ th to  $\frac{1}{625}$ th of an inch), characterized by their quadrangular base and tail-like extremity, the latter pointing outwardly, the smallest cells being the most superficial, and the cells constituting the so-called nuclear layer situated beneath the pyramidal cells and about 10 micro-millimetres ( $\frac{1}{2500}$ th of an inch) in diameter. The pyramidal cells are more numerous and larger in the anterior portion of the hemispheres in the convolutions of the frontal lobe, for example, the cells of the nuclear layer in the occipital and temporal lobes. Certain so-called giant pyramidal cells, probably motor in function, like those of the anterior cornu of the spinal cord, are also found more particularly in the posterior portion of the frontal lobe in the anterior convolution, the processes of which appear to be prolonged downward as the axis-cylinders traversing the antero-lateral columns of the spinal cord emerging from the latter as the anterior roots of the spinal nerves, while other cells, having no processes or axis-cylinders, are found more especially in the posterior part of the hemispheres in the occipital lobe. Although the convolutions or gyri and the fissures or sulci do not run in exactly the same manner in different brains, and are not symmetrically disposed even in the two hemispheres of the same brain, nevertheless the general disposition is so constantly the same that the most important of them

can be readily recognized and identified, and on account of their supposed functional importance demand at least a brief description. The most striking fissure observable, if the hemisphere be viewed laterally, both on account of its depth and constancy, it existing not only in man but in all animals whose brain is fissured at all, is the fissure of Sylvius. Beginning as a transverse furrow on the under side of the brain, it runs thence outward, backward, and upward, separating the temporal (T, Fig. 403) from the frontal lobe (F), and divides on the outer side of the hemisphere into an anterior (S) and posterior (S') branch, the convolutions included between these two branches, and known as the operculum,

FIG. 403.



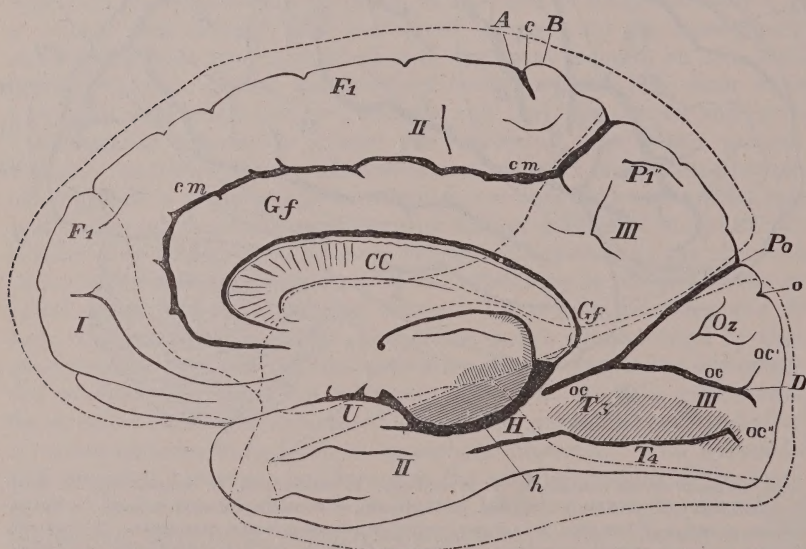
Outer surface of the left hemisphere. F. Frontal lobe. P. Parietal lobe. O. Occipital lobe. T. Temporo-sphenoidal lobe. S. Fissure of Sylvius. S' Horizontal, S'' Ascending ramus of the same. c. Sulcus centralis or fissure of Rolando. A. Anterior central or ascending frontal convolution. B. Posterior central or ascending parietal convolution. F<sub>1</sub> Superior, F<sub>2</sub> Middle, and F<sub>3</sub> Inferior frontal convolution. f<sub>1</sub> Superior, and f<sub>2</sub> Inferior frontal sulcus; f<sub>3</sub> Sulcus præcentralis. P<sub>1</sub> Superior parietal of postero-parietal lobule, viz : P<sub>2</sub> Gyrus supramarginalis, P'<sub>2</sub> Gyrus angularis. *ip.* Sulcus intraparietalis. *cm.* Termination of the callosal-marginal fissure. O<sub>2</sub> first, O<sub>1</sub> second, O<sub>2</sub> third occipital convolutions. *po.* Parieto-occipital fissure O. Sulcus occipitalis transversus, O Sulcus occipitalis longitudinalis inferior. T<sub>1</sub> first, T<sub>2</sub> second, T<sub>3</sub> third temporo-sphenoidal convolutions. t<sub>1</sub> first, t<sub>2</sub> second temporo-sphenoidal fissures. (After ECKER and DURET.)

covering the insula or island of Reil. An important fissure, readily identified on account of its constant course, is the fissure (c) of Rolando, or central fissure, passing from about the middle line of the hemisphere downward, outward, and forward, reaching very nearly the fissure of Sylvius, and serving to divide the frontal from the parietal lobe. The fissure of Rolando is bordered by two important convolutions running



parallel with itself and known as the anterior and posterior central convolutions, or the ascending frontal and ascending parietal convolutions. Through the very constant presence of the long superior frontal ( $f_1$ ) and inferior frontal fissure ( $f_2$ ) the latter running into the precentral fissure ( $f_3$ ), the anterior portion of the frontal lobe naturally divides itself into the superior ( $F_1$ ), middle ( $F_2$ ), and inferior ( $F_3$ ) frontal convolutions. Through the presence of the first and second temporo-sphenoidal fissures in the same manner, the temporal lobe ( $T$ ) is divided into the first ( $T_1$ ), second ( $T_2$ ), and third ( $T_3$ ) temporo-sphenoidal convolutions. The most important fissure of the parietal lobe ( $P$ ) is the intraparietal fissure ( $ip$ ). Starting from the posterior central convolution, it extends backward and downward, and dividing the parietal lobe into the superior ( $P_1$ ) and inferior ( $P_2$ ) parietal lobules, terminates toward the posterior extremity of the hemisphere. Beneath the intraparietal fissure, and as constituent parts of the inferior parietal lobule, are situated two important convolutions, the supra-marginal ( $P_2$ ) convolution arching around the fissure of Sylvius and the angular ( $P'_2$ ) convolution around the first temporo-sphenoidal

FIG. 404.



Inner surface of right hemisphere. The regions bounded by the line (-----) represent the territories over which the branches of the anterior cerebral artery are distributed. The regions bounded by the line (-----) represent the territories over which the branches of the posterior cerebral artery are distributed. CC. Corpus callosum, longitudinally divided. Gf. Gyrus fornicatus. H. Gyrus hippocampi. h. Sulcus hippocampi. U. Uncinate gyrus. cm. Sulcus callosus-marginalis. F<sub>1</sub>. Median aspect of the first frontal convolution. c. Terminal portion of the sulcus centralis, or fissure of Rolando. A. Anterior. B. Posterior central convolution. P<sub>1</sub>'. Præcuneus. Oz. Cuneus. Po. Parieto-occipital fissure. o. Sulcus occipitalis transversus. oc. Calcarine fissure, oc' Inferior ramus of the same. D. Gyrus descendens. T<sub>4</sub>. Gyrus occipito-temporalis lateralis (lobulus fusiformis). T<sub>5</sub>. Gyrus occipito-temporalis medialis (lobulus lingualis). (After ECKER and DURET.)

fissure. The parietal is separated from the occipital (O) lobe by the parieto-occipital (Po) fissure, the latter being, however, just visible from

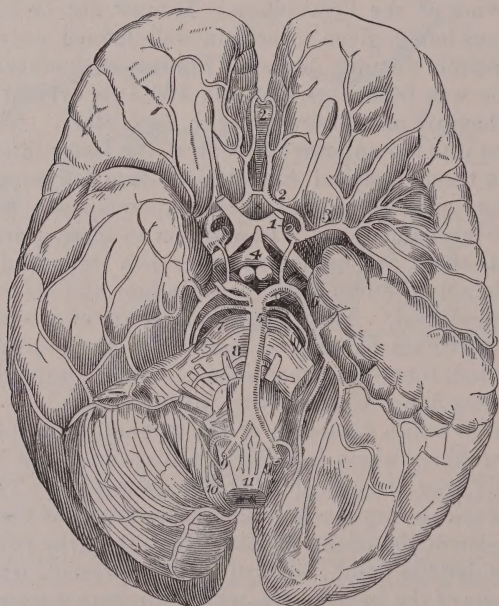
a lateral view, should be viewed from the mesial surface of the hemisphere, as in Fig. 404, where it (Po) will be observed to descend downward and inward, separating the cuneus (Oz) from the præcuneus (P'<sub>2</sub>) and terminating in an acute angle in the calcarine fissure (oc), the latter fissure being so called on account of its marking the inner concave border of the calcarius or hippocampus minor in the posterior cornu of the lateral ventricle. The occipital lobe (O) is made up of the first (O<sub>1</sub>), second (O<sub>2</sub>), and third (O<sub>3</sub>) occipital convolutions, the first occipital being separated from the second occipital convolution by the transverse occipital fissure (O), and the second occipital convolution from the third by the inferior longitudinal occipital fissure (O<sub>2</sub>). As the calcarine fissure (oc, Fig. 404) does not run into the hippocampal (p) fissure, it will be observed that the convolution lying above the corpus callosum, and known as the gyrus fornicatus (Gf), passes continuously into the convolution of the hippocampus (H). The latter convolution terminates anteriorly in a crook-like extremity or crotchet, the so-called uncus gyri fornicati or subiculum cornu ammonis (V). Below the calcarine fissure are situated two convolutions, the lobulus fusiformis (T<sub>4</sub>) and lobulis lingualis (T<sub>5</sub>), separated by the occipito-temporal fissure, while above the gyrus fornicatus (Gf) is separated from the mesial surface of the first (F<sub>1</sub>) frontal convolution by a well-marked fissure, the callosomarginal (cm), which, like the parieto-occipital fissure, is also just visible from a lateral view of the hemisphere. It must not be supposed from the fact of names being given to certain well-defined convolutions that the latter are entirely distinct, or do not run into each other; on the contrary, as may be seen from Figs. 403 and 404, it is evident that directly or indirectly they are all continuous with each other. Thus the third frontal (F<sub>3</sub>) runs into the anterior (A) central, the latter into the posterior (B) central, the three occipital convolutions into the superior parietal lobule (P), the angular gyrus and third temporo-sphenoidal (T<sub>3</sub>) convolutions respectively, and so on. In addition to these principal fissures just mentioned, there are numerous other less important ones which increase considerably the number of convolutions and obscure somewhat those already described. That these fissures are of a secondary character, however, becomes at once evident when the arachnoid and pia mater are removed, they being then seen to be mere superficial indentations and not deep fissures penetrating into the brain.

The internal or white substance of the cerebral hemispheres is composed largely of fibres which in general radiate from the basal ganglia internally to the gray or cortical substance outwardly. The amount of white substance varies very much in different portions of the hemisphere, thus, in the region of the island of Reil, where the gray substance penetrates to a considerable depth, but little of it is present, whereas, in the posterior portions of the hemisphere, where the gray matter is relatively less well developed, the white substance is present in great quantity. The fibres of which the white substance consists may be said to be essentially of three kinds: First, commissural fibres, such as those composing the corpus callosum or the broad commissure connecting the two hemispheres at the bottom of the great longitudinal fissure or the anterior commissure situated a little in front of the thalami optici and



spreading out from the latter into the lower and anterior parts of the temporal lobes. Second, association fibres, or fibres which, lying just beneath the gray matter, connect the different convolutions of the same hemisphere. Third, medullary fibres including both the indirect fibres passing from the medulla through the crura cerebri and terminating in the corpora striata and thalami optici, and the fibres of the corona radiata, which beginning in the basal ganglia spread out to terminate in the convolutions and the direct fibres which, beginning in the convolutions about the fissure of Rolando and probably motor, pass downward through the middle of the crura to the pyramid tracts of the cord, or beginning in the cord pass upward along the outward border of the crura to terminate in the convolutions of the occipital lobe, and probably sensory in function. One of the most striking facts with reference to the cerebral hemispheres, the bulk of the latter being taken into consideration, is the large amount of blood which they receive, one-fifth of the whole mass of the blood, indeed, according to Haller,<sup>1</sup> going to the encephalon. The manner in which the blood is distributed to the brain is also very remarkable, the branches of the basilar (5) and internal (1) carotid arteries anastomosing so freely, as the circle of Willis (Fig. 405), that the

FIG. 405.



Circle of Willis. (QUAIN and SHARPEY.)

supply of blood to any one part of the brain is not interrupted, even though the principal branch supplying such a part be obstructed. The

<sup>1</sup> *Elementa Physiologie.*

importance of this peculiarity in the distribution of the cerebral blood-vessels becomes at once apparent when it is remembered that with the cessation of the blood supply the functional activity of the brain at once ceases, and it may be appropriately mentioned in this connection that while in all probability the energy of the brain depends largely on the size of its arteries and the freedom with which the blood circulates through them, the special manifestation of brain power depends upon the particular areas of distribution. It has already been mentioned that the gray matter of the nervous system is more vascular than the white, and that in all probability it is in the gray or vascular substance that the nervous force is generated, the white or fibrous substance transmitting it. The significance, therefore, of the development of the convolutions just described produced through the invaginating of the gray substance into the white, together with their pia mater or vascular tunic, thereby insuring a far greater supply of blood than would be possible if the brain were smooth, becomes evident. Further, when it is borne in mind that the brain is enclosed in a bony unyielding case, and that the amount of blood sent to the brain from the heart must vary with the force of the latter, and that the cerebral disturbances ensue with any increase or diminution in pressure it might be anticipated that some provision must exist by which a uniform pressure within the cerebral substance is maintained. The latter function appears to be fulfilled by the cerebro-spinal fluid found in the subarachnoid cavity of the brain and cord, since if this fluid be withdrawn from a living animal, cerebral disturbances attributable to changes in pressure ensue. The cerebro-spinal fluid amounts to at least two ounces, and probably more, and appears to be as rapidly absorbed as produced, and as it readily passes from the subarachnoid space through the foramen of Magendie or the triangular orifice in the pia mater situated at the inferior angle of the fourth ventricle into the ventricles of the brain or the central canal of the cord, it evidently serves to equalize the pressure in the cranial cavity, merely allowing bloodvessels to expand and contract within such limits as do not induce any marked change in the pressure to which the brain substance is usually subjected.<sup>1</sup> The entire encephalon in the adult male brain weighs on an average about fifty ounces, that of the female a little less, about forty-four ounces. On this supposition, the relative weights of the cerebrum, cerebellum, etc., are as follows:

TABLE LXXIV.<sup>2</sup>

| Average weight.                           | Male.                | Female.              |
|-------------------------------------------|----------------------|----------------------|
| Cerebrum . . . . .                        | 43.98 oz.            | 38.75 oz.            |
| Cerebellum . . . . .                      | 5.25 "               | 4.76 "               |
| Pons and medulla . . . . .                | 0.98 "               | 1.01 "               |
| Entire encephalon . . . . .               | 50.21 "              | 44.52 "              |
| Ratio of cerebrum to cerebellum . . . . . | 1 to 8 $\frac{1}{4}$ | 1 to 8 $\frac{1}{4}$ |

The human brain is absolutely heavier than that of any other animal except the elephant and the cetacea, the brain of the elephant usually

<sup>1</sup> Magendie: *Journal de Physiologie*, tome v. p. 27, Paris, 1825; tome vii. pp. 1-66, 1827.

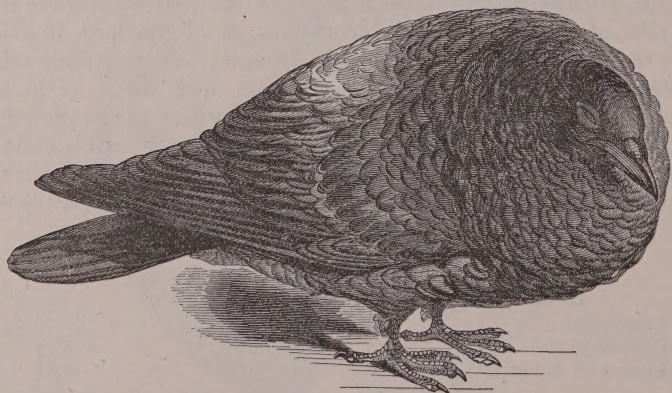
<sup>2</sup> Quain's *Anatomy*, 8th ed., vol. 2d, p. 581.



weighing from eight to ten pounds<sup>1</sup> or even more, that of the young male elephant which recently died at the Philadelphia Zoological Gardens having been found by the author to weigh immediately after removal from the skull ten and a half pounds. The brain of the whale weighs about five pounds;<sup>2</sup> that of a grampus delphinus, as found by the author, seven pounds. Relatively, however, to the size of the body the brain is larger in certain birds and mammals than in man, as, for example, in the canary bird, field mouse, and ousitite monkey. With reference, however, to the size of the nerves given off from its base, the brain of man is larger than that of any other animal without exception.

The brain consists chemically<sup>3</sup> of about 75 per cent. of water, 15 of fats, 7.5 albuminoids, 1.5 of salts, 1 of extractives, including such principles as cerebrin ( $C_{17}H_{33}NO_3$ ), lecithin ( $C_{44}H_{90}NPO_9$ ), cholesterin, fats, fatty acids, phosphorus, sodium chloride, salts of lime, potash, and magnesia. The relative amounts in which cholesterin, fat, and cerebrin are found in the gray and white substance of the brain are worthy of mention. Thus, while gray substance contains 18.7 per cent. of cholesterin and fat and only 0.5 of cerebrin, the white substance contains 51.9 per cent. of cholesterin and 9.5 of cerebrin. The quantity of phosphorus is very noticeable, amounting to from 1.3 to 1.7 per cent. Its presence as an indispensable condition of a healthy brain cannot be overestimated. Indeed, it has been truly said "without phosphorus no thought."<sup>4</sup> In considering the functions of the medulla, pons, cerebellum, and basal ganglia, we have necessarily anticipated somewhat, by a process of exclusion, the functions of the cerebral hemispheres. It only now remains for us to offer the positive evidence bearing upon the questions and confirming the general conclusions already reached by the manner just mentioned.

FIG. 406.



Pigeon, after removal of the hemispheres. (DALTON.)

If the cerebral hemispheres be removed in a pigeon, for example, the animal at once falls into a condition of stupor, its whole appearance

<sup>1</sup> Cyclopædia of Anat. Phys., vol. iii. p. 664. Lond. 1839-47.

<sup>2</sup> Rudolphi : Grundriss der Physiologie, B. ii. S. 12. Berlin, 1823.

<sup>3</sup> Carpenter's Physiology, 1881, p. 529.

<sup>4</sup> Moleschott : Lehre der Nahrungsmittel, S. 115. Erlangen, 1850.

being very peculiar and most characteristic (Fig. 406). With its head almost buried within the feathers of the neck, with closed eyes, the pigeon stands sufficiently firmly, but without moving, apparently utterly indifferent to its surroundings. From time to time it opens its eyes, stretches its neck, or smooths its feathers, but soon again relapses to its former condition of apathy. That the pigeon, however, still feels there can be no doubt. Pinch its neck or one of its toes and a persistent effort is made to withdraw the part from the grasp. Fire off a pistol, the pigeon will open its eyes and turn its head round as if it had heard the report and was looking whence it came. The report of the pistol, however, causes no alarm, for the pigeon makes no effort to escape. While the animal undoubtedly hears and sees, the sensations do not give rise to the usual ideas associated with or developed out of them, the pigeon feels but does not perceive the sensation of sound; the report of the pistol does not give rise to any idea of danger usually associated with the production of sound. In the same way the presence of food, though seen and smelt by the pigeon, does not excite the idea of hunger, the animal making no effort to feed, starving to death amidst plenty. That this entire loss of memory, volition, and conscious intelligence, following loss of the cerebral hemispheres in a pigeon and a mammal is not due simply to the effects of shock, hemorrhage, etc., is shown not only by the entirely different effect following destruction of the cerebellum, but that a pigeon from which the cerebral hemispheres have been removed can be kept alive for months by artificial feeding, and a mammal usually for a short period, and, although the effects of shock have long since passed away, nevertheless, the animal never regains its intelligence, remaining ever afterward in this characteristic condition of stupor and apathy. Although the effects of destruction or compression of the cerebral hemispheres in man, whether due to disease or injury, are not as well established as in the case of birds and mammals through the imperfect localization of the disease, the basal ganglia, etc., being usually involved as well as the cerebral hemispheres; nevertheless, a sufficient number of cases have been observed by pathologists which show that loss or compression of the cerebral hemispheres in man involves, as in the case of birds and mammals, the loss of memory, volition, conscious intelligence, the negative functions, however, remaining unimpaired. Among such cases may be mentioned that of the sailor related by Sir Astley Cooper,<sup>1</sup> who, having fallen, probably from the yard-arm, was picked up on the deck insensible, practically deprived of all powers of mind, volition, or sensation, in which condition he remained for thirteen months, being kept alive all this time by artificial feeding, the grinding of the teeth and the sucking of the lips indicating to his attendants the necessity of giving food and drink. During this period the man lived almost entirely a vegetable existence, the only movements he made, with the exceptions of the lips, etc., being with the fingers, which he moved to-and-fro to the time of the pulse. In this condition the sailor was seen by Dr. Cline, the famous surgeon of the day, who, satisfying himself that a depression in the skull existed,

<sup>1</sup> Lectures on the Principles and Practice of Surgery, p. 138. Philadelphia, 1839.



trephined, and with the happy result that within a short time after the operation the patient was able to get out of bed, talk, and tell where he came from, his mind having been restored through the removal of the pressure exerted by the depressed bone upon the cerebral hemispheres.

In general, it may be said that injury or disease of the cerebral hemispheres in man entails disturbance or loss of the intellectual powers, according to the seat and extent of the lesion. Impairment and then loss of memory, weakening and failure of the reasoning powers and of the judgment, invariably follow disease or injury of the cerebral hemispheres, while the facts that under such circumstances there is no loss of sensation or motor power, and that the vegetative functions also remain unimpaired, as in the case of idiots and the insane, clearly show that the cerebral hemispheres are indispensable to the manifestation of the intelligence. On the other hand, the fact already mentioned of animals deprived of their cerebral hemispheres living indefinitely when supplied with food, and of human beings being born anencephalous and yet were kept alive some time, and who sucked and cried like ordinary infants, proves that the cerebral hemispheres are not concerned in the performance of those functions not involving intellection, which have been assigned to other parts of the encephalon. That the intellectual powers depend upon the development of the encephalon is also shown by the facts of comparative anatomy, the encephalon of the more intelligent animals being much heavier both absolutely and relatively, with reference to the weight of the body, than that of the less intelligent ones. Thus, in fishes the ratio of the encephalon to the body is as 1 to 5668, in the reptiles as 1 to 1321, in birds as 1 to 212, in mammals 1 to 189,<sup>1</sup> and in man as 1 to 50, supposing the body of the man to weigh 150 pounds and the brain about 48 ounces, or three pounds. Further, the brain of the lower races of mankind is not as heavy as that of the higher and more intellectual ones, weighing on an average only about 46 ounces, and is much less bulky, occupying perhaps a space within the skull of only 63 cubic inches,<sup>2</sup> while that of the higher races may occupy a space of 114 cubic inches.<sup>3</sup> It is also well known that individuals distinguished by great intellectual power possessed large and heavy brains, thus, the brain of Abercrombie weighed 63 ounces,<sup>4</sup> that of Cuvier 64.33 ounces.<sup>4</sup> On the other hand, the brain of idiots has been found in some instances to weigh not more than 20 ounces. It will be observed also from a comparison of the brain of the lower with that of the higher vertebrates, that it is the greater development of the cerebral hemispheres in the latter to which are due the greater bulk and weight of the encephalon. Thus, as we pass from the brain of the fish (Fig. 407) to that of the reptile (Fig. 408), from the brain of the reptile to that of the bird (Fig. 409), from the latter to the brains of mammals (Fig. 410), including that of man, one cannot but be impressed with the fact that the cerebral hemispheres become successively more and

<sup>1</sup> Leuret: *Anatomie Comparée du Systeme Nerveux*, pp. 153, 234, 284, 422. Paris, 1839.

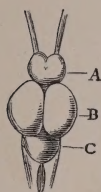
<sup>2</sup> Morton: *Crania Americana*, p. 253. Philadelphia, 1839.

<sup>3</sup> Edinburgh Med. and Surg. Journal, 1845, vol. lxiii. p. 448.

<sup>4</sup> "Trois livres onze onces quatre gros et demi," is the number given in the account of the autopsy of Cuvier in the *Archives générales de Médecine*, tome xxix. p. 144. Paris, 1832.

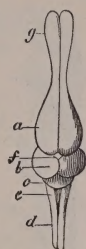
more developed, until in the monkeys (Fig. 411) (excepting young and possibly also adult anthropoids) and in man they completely cover the

FIG. 407.



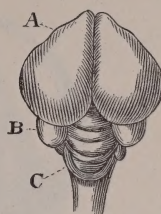
Brain of carp. A. Cerebral hemispheres. B. Optic lobes. C. Cerebellum.

FIG. 408.



Brain of lizard. (OWEN.)

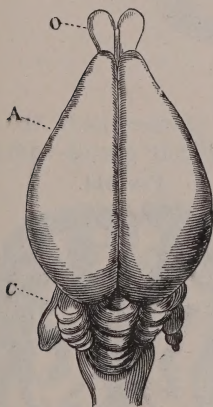
FIG. 409.



Brain of the pigeon. A. Cerebral hemispheres. B. Optic lobes. C. Cerebellum. (FERRIER.)

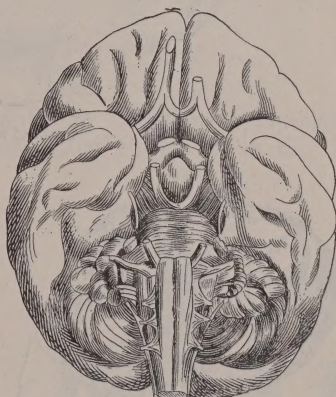
cerebellum. Further, it may also be seen from such a comparison that while the brain in fish, reptiles, birds, and the lower orders of animals, such as the marsupiala, rodentia, suenia (Fig. 412), etc., is smooth

FIG. 410.



Brain of the rabbit. A. The smooth cerebral hemisphere. B. The olfactory bulb. C. The cerebellum. (FERRIER.)

FIG. 411.



Base of brain of baboon. (OWEN.)

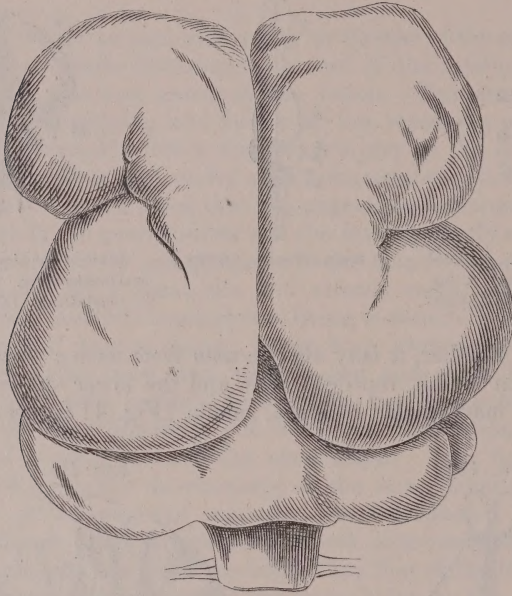
or nearly so, in the higher orders, including the proboscidea, cetacea, the ungulata (Figs. 413, 414), the carnivora and primates (Fig. 415), it is more or less convoluted. Indeed, so much is this the case that in the proboscidea it is particularly convoluted, even more so than in man. In general, it may be said that the development of the intellectual powers depends not only upon that of the encephalon, but more particularly upon that of its cerebral hemispheres, and especially, as affirmed long ago by Erasistratus,<sup>1</sup> upon the number and depth of the

<sup>1</sup> Galenus De Usu Partium, Lib. 8, Cap. 13.



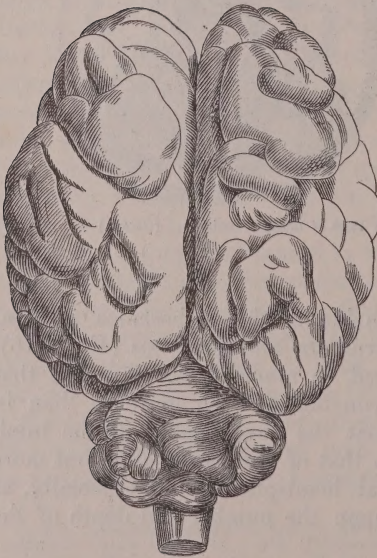
convolutions of the gray matter of the same. Further, in the savage races of mankind, characterized by a low order of intelligence, the con-

FIG. 412.



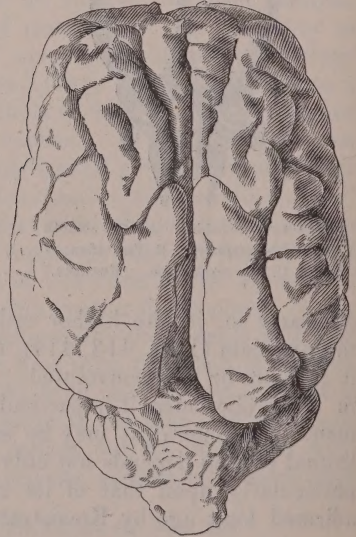
Brain of manatee.

FIG. 413.



Brain of the horse. (OWEN.)

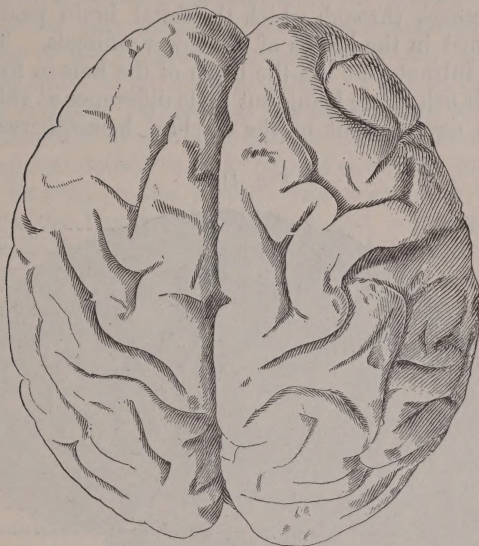
FIG. 414.



Brain of peccary.

volutions are not so deep, are less numerous, and are more simply disposed than in the civilized races distinguished by the develop-

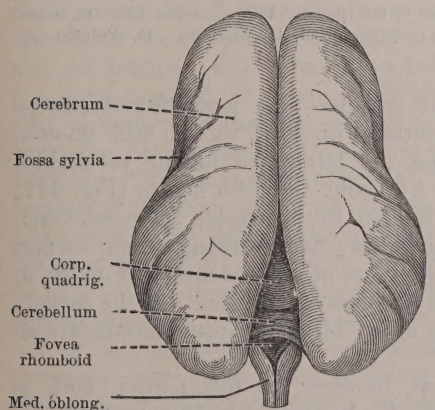
FIG. 415.



Brain of the orang.

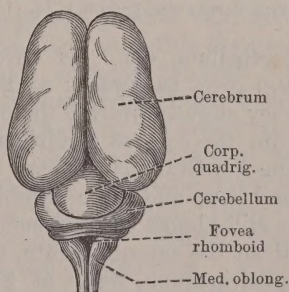
ment of their mental faculties, while in individuals especially remarkable among the latter for intellectual power, as in the case of

FIG. 416.



Brain of human embryo, three months.

FIG. 417.



Brain of human embryo, five months.

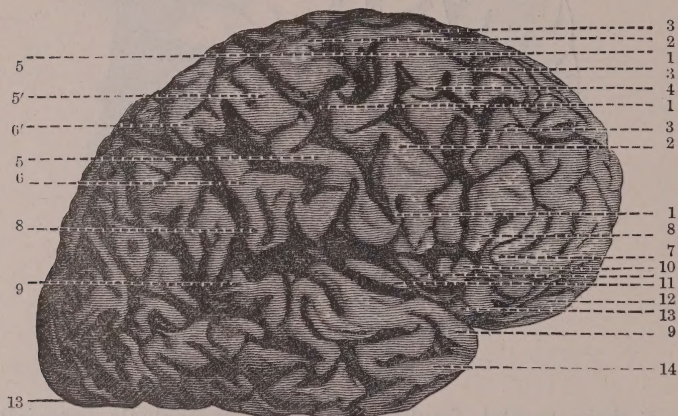
Gauss,<sup>1</sup> for example, one of the most distinguished mathematicians that ever lived, the convolutions of the cerebral hemispheres were found to

<sup>1</sup> Quain : Anatomy, 1878, vol. ii. pp. 529, 581.



be very numerous and deep, and far from simply arranged. On the other hand, in idiots the convolutions are few, comparatively superficial, and simply disposed. The development of the brain also confirms the conclusions based upon the facts of comparative anatomy and ethnology, the transitory stages through which the foetal brain passes being permanently retained in the brains of the lower animals. Thus, at about three weeks of intrauterine life the brain of the human foetus resembles that of the adult fish, there being but little difference at this early period in the relative development of the cerebral hemispheres, optic lobes,

FIG. 418.



Lateral view of the right cerebral hemisphere. 1 Fissure of Rolando. 2. Ascending frontal convolution. 3. Superior, 3', middle, and 7, inferior frontal convolutions. 4. A bridging convolution between the superior and middle frontal convolutions. 5. Ascending parietal convolution. 6, 8. Supramarginal convolution (8 in front points to part of the inferior frontal convolution). 9, 9. Superior temporo-sphenoidal convolution. 10, 11, 12. Convolutions of the island of Reil, or central lobe. 13. Orbital convolutions. 14. Lower extremity of middle temporo-sphenoidal convolution. 15. Occipital lobe. (From SAPPÉY after FOVILLE.)  $\frac{1}{2}$ .

cerebellum, etc. As development advances the hemispheres enlarge and grow backward; at three months (Fig. 416), though still smooth, they slightly overlap the optic lobes, the latter not having yet divided into the corpora quadrigemina. At about the fifth month (Fig. 417) the cerebral hemispheres in the human foetus overlap the cerebellum, and here and there exhibit a rudimentary fissure, though their surface is still almost entirely smooth, as in those of the rodentia. Finally, at about the seventh month, the optic lobes are subdivided into the corpora quadrigemina, while at full term or at birth the convolutions are all formed.

The brain of the human foetus, however, at this period, both as regards the number, depth, and simplicity of arrangement of the cerebral convolutions, resembles rather the brain of the chimpanzee than that of the adult man, while the brain of the uneducated child resembles, in similar respects, that of the savage races of mankind rather than that of the civilized ones; a physical correspondence in harmony with their intellectual acquirements. While the facts of

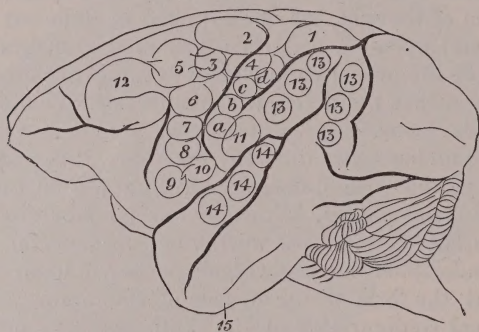
experiment, pathology, comparative anatomy, etc., with but few exceptions, and those usually more apparent than real, undoubtedly agree in establishing the view that associates intellectual power with the development of the cerebral hemispheres, and more particularly with that of the convolutions, or the gray matter of the same, it must be borne in mind that the quality of the chemical composition of the latter is quite as important a condition as its mere quantity. Further, that the exercise of the mental faculties necessitates the connections between the gray or vascular substance of the convolutions and the fibres of the white substance being maintained in their normal condition, just as the action of a muscle depends on the position and manner of insertion; and, above all, upon the free supply of blood and active circulation, both that the materials for the nourishment of the hemispheres and the production by them of thought, may be supplied in sufficient quantity, and that the effete and worn-out materials incidental to mental activity may be carried away to the proper emunctories as rapidly as produced. As we have already seen that the different structures of which the encephalon consists, medulla, pons, cerebellum, basal ganglia, cerebral convolutions, etc., have undoubtedly different functions, it is reasonable, therefore, to suppose that the different convolutions, or the gray matter of the cerebral hemispheres, have also special faculties or functions. Phrenology has, therefore, a basis worthy of consideration. Phrenology, however, as understood by the vulgar, is based upon the untenable assumption that the form of the surface of the brain can be inferred from the external configuration of the skull, that any protuberance, or "bump," of the latter is to be taken as an indication of a similar excessive development of the former, and the possession of some particular well-developed mental faculty. Apart, however, from the facts that the skull consists of two tables, and that the outer surface of the brain is separated from the inner surface of the skull by the dura mater, arachnoid, pia mater, and cerebro-spinal fluid, the latter variable, in quantity, the figure of the brain, except in a general way, does not correspond to the figure of the skull. So much so is this the case that in certain animals, as in the elephant, for example, through the enormous development of the frontal sinuses the anterior portion of the skull is no indication of the form of the brain whatever. Further, the surface of the brain is not elevated into bumps, the convolutions, as we have seen, being formed through the invagination, or dipping down of the gray matter into the white. Even though, then, osseous "bumps" be ever so well developed, there are never any cerebral "bumps" with special functions or faculties corresponding to the osseous ones. Phrenology, as such, must be relegated, then, to the charlatan and itinerant showman, who amuse their audience by feeling their heads, and illustrating their views by showing plaster casts of the heads of Napoleon, Schiller, noted murderers, idiots, and the like. Within recent years, however, another kind of phrenology has been developed and established, more or less satisfactorily based upon entirely different methods of investigation,<sup>1</sup> such as exposing the brain in a living animal, and

<sup>1</sup> Fritsch and Hitzig: *Archiv f. Anat., Physiologie, etc.*, S. 300. Leipzig, 1870. Ferrier: *Functions of the Brain*, 1876. Carville and Duret: *Archives de Physiologie* 2eime série, tome ii. p. 352. Paris, 1875. Dalton: *New York Medical Journal*, 1875, p. 225.



stimulating with a weak electrical current a particular convolution, and so determining whether the latter is excitable, and whether its stimulation causes sensory or motor effects; or, destroying a particular convolution by cutting, corrosion, etc., and observing whether the animal is deprived of any of its faculties, and so learning whether the convolution has motor or sensory functions. By such experimental methods particular functions have been assigned in animals to the different convolutions of the brain, and there can be little doubt that such convolutions of the brain in man as are homologous with the brain in monkeys and the higher mammalia have essentially the same functions as in the latter; the results obtained by post-mortem examination and the

FIG. 419.



The left hemisphere of the monkey. (FERRIER.)

clinical study of disease of the brain in man confirm the results obtained by experimentation upon animals; destruction of the convolutions by injury or disease entailing the loss of motor or sensory faculties.<sup>1</sup> Thus, electrical irritation of the convolutions bordering the fissure of Rolando in the brain of the monkey (Fig. 419, 1, 2, 3, 4, 5, 6, 7, 8, *a*, *b*, *c*, *d*) and in man (Fig. 420), at least in the only case recorded,<sup>2</sup> gives rise to certain well-defined constant movements of the hands, feet, arms, legs, facial muscles, mouth, and tongue, on the opposite side of the body.

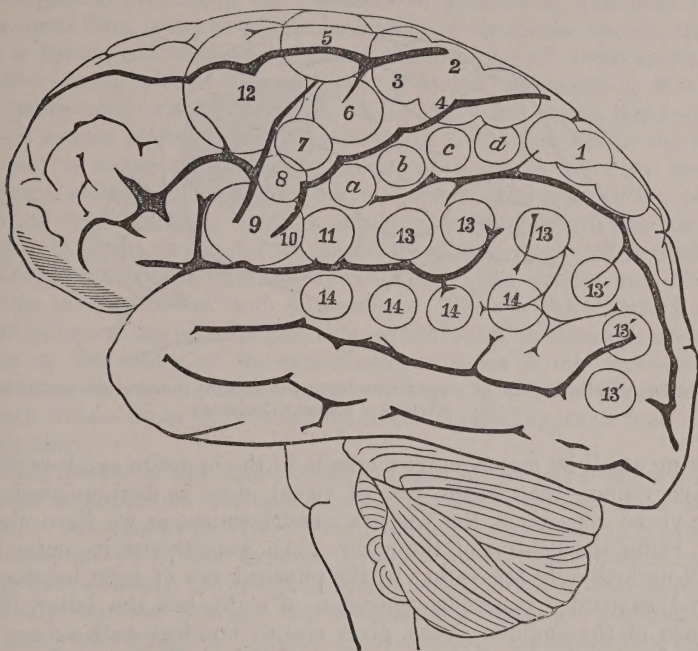
That the muscular contractions induced through electrical stimulation of these or other convolutions are not due to an escape or diffusion downward of the electrical current, and so affecting the corpus striatum, etc., is shown, apart from the fact that stimulation by chemical agents produces the same effect, by several considerations, among which may be mentioned the feebleness of the current used, the close approximation of the electrodes, the imperfect conductivity of the brain substance, the muscular contractions occurring on the opposite side of the body, and not occurring at all when other convolutions were stimulated. That these convolutions are in reality motor centres, constituting the indispensable physical substratum for the volitional, psychical initiation of movements corresponding to those induced by electrical stimulation,

<sup>1</sup> Ferrier: *Localization of Cerebral Disease*, p. 42. London, 1879. Grasset: *Des Localisations dans les Maladies Cérébrales*, p. 143. Paris, 1880. Charcot: *Leçons sur les Localisations dans les Maladies du Cerveau*, p. 166. Paris, 1878. *Rendu Revue des Sciences Médicales*, tome xiii. p. 314. Paris, 1879.

<sup>2</sup> Bartholow: *American Journal of the Medical Sciences*, April, 1874.

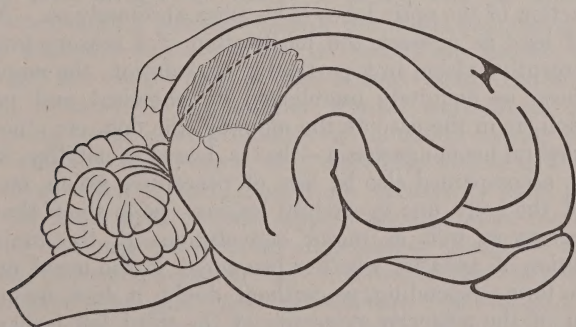
the latter acting in the same manner as the stimulus of the will, is further shown by the fact that destruction of these convolutions in the

FIG. 420.



Lateral view of the human brain. The circles and letters have the same significance as those in the brain of the monkey, Fig. 453. (FERRIER.)

FIG. 421.



Brain of dog; showing excision of angular convolution and two adjacent anterior convolutions on left side. Blindness of right eye. (FERRIER.)

monkey<sup>1</sup> by experiment (Fig. 421) and in man<sup>2</sup> by disease causes complete hemiplegia of the opposite side of the body without affecting

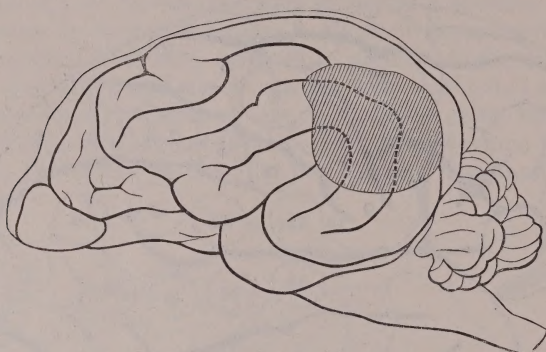
<sup>1</sup> Ferrier: Functions of the Brain, 1876, p. 201.

<sup>2</sup> Lepine: De la Localisation dans les Maladies Cérébrales, p. 33. Paris, 1875. Gliky: Deutsches Archiv für klin. Med., Dec. 1875.



sensation. On the other hand, destruction in the monkey<sup>1</sup> of certain convolutions, like the angular gyrus (Fig. 422), for example, while not

FIG. 422.



Brain of dog, showing excision of angular convolution and adjacent posterior convolution in right side. Blindness of left eye. (FERRIER.)

affecting at all its motor powers, entails in the opposite eye loss of perceptive vision—that is, the loss of visual ideas as distinguished from mere visual sensations, the corpora quadrigemina, as we have already seen, being the centres of the latter. An animal with its optic lobes intact undoubtedly sees—that is, the physical ray of light becomes the mental subjective conscious sensation of sight, but the latter, in the absence of the angular gyrus, gives rise to no ideas such as are normally developed out of the sensation of light. Under such circumstances familiar objects are seen, but do not suggest the ideas of pleasure or pain, for example, usually associated with them. In a word, the animal sees, but does not perceive, it is only psychically blind; with the destruction of the optic lobes it becomes absolutely so. Now, while in man, at least at present, the localization of a sensory function like that of perceptive vision in a particular convolution, the angular gyrus, has not been as definitely established by chemical and pathological investigation, as in the case of the monkey, the dog, etc., nevertheless, cases of cerebral hemianæsthesia—that is, loss of sensibility, without loss of motion, accompanied also by loss of perceptive vision, on the opposite side of the body, due to cerebral lesions—go to show<sup>2</sup> that there are special sensory as well as motor convolutions in the brain of man. The condition of aphasia, whether presented in the usual, or agraphic, or amnesic form, depending, as, without doubt, it does, upon disease in the region of the posterior extremity of the third left frontal convolution, where the latter abuts on the fissure of Sylvius, and overlaps the island of Reil, is a most convincing argument in favor of the view of the cerebral functions being localized in the convolutions of the hemispheres. Merely referring incidentally to the researches of Petit,<sup>3</sup>

<sup>1</sup> Ferrier, *ibid.*, p. 167.

<sup>2</sup> Ferrier, *op. cit.*, pp. 170, 181.

<sup>3</sup> Recueil d'observations d'anatomie et de chirurgie, p. 74. Paris, 1766.

Bouillaud,<sup>1</sup> Dax,<sup>2</sup> Broca,<sup>3</sup> Hughlings Jackson,<sup>4</sup> etc., upon the subject of aphasia, the detailed consideration of which belongs rather to the study of clinical medicine and pathological anatomy, it may be briefly said that a person presenting the condition of aphasia as exhibited in its most usual form is deprived of the faculty of articulate speech, though such a person comprehends perfectly the meaning of words spoken by others; having a clear idea of language and of the meaning of words, and being able to write perfectly well. In other cases, however, the patient cannot express ideas in writing, or cannot remember the words wanted; in those of aphasia, agraphia, or amnesia, the idea even of language is lost. That the inability to speak exhibited by the person suffering from aphasia, whether simple or combined with the amnesic or agraphic form, is not due to paralysis of the muscles of articulation is shown by the fact that the aphasic individual makes use of these muscles in mastication and deglutition. Though the centre for the coördination of the muscles effecting articulation be diseased, since the action of the centre of the articulating muscles is bilateral—that is, the centre in one hemisphere innervating the muscles of articulation of both sides—there is no difficulty in understanding that such should be the case.

While disease of the centre of articulation of the left hemisphere, for the reason just given, does not entail paralysis of the muscles of articulation, it does entail paralysis of articulation or speech, the centre for the coördination of the muscles involved in the production of speech being then affected. When it is remembered, however, that speech is gradually acquired through the constant and continual association in the mind of sounds or written signs with the corresponding spoken words, that the acquisition of speech, physiologically speaking, is the development in the brain of an organic nexus between the sound or symbol, and the articulation, it becomes intelligible why if this nexus be broken, that, though the sound be heard and the symbols seen, and the corresponding ideas developed, the words expressing the ideas cannot be uttered,—the individual is speechless, because, as Ferrier expresses it,<sup>5</sup> the motor part of the sensori-motor cohesion, sound-articulation situated in the inferior frontal convolution, is broken. Further, owing to the close proximity of the motor centre of the hand and facial muscles, it is easy to see, therefore, why dextral and facial paralysis are so often present, though not necessarily so in the case of aphasia. At first sight it may appear strange that the centre for coördinating the muscles effecting articulation should be located exclusively in one hemisphere; in reality, however, there is nothing more strange in this than that most persons are right-handed. Dextral movement, like articulate speech, is gradually acquired, and there is no more reason to doubt that in the absence of the coördinating centres of articulation of the left hemisphere that of the right could be educated, than that in the absence of the right hand one could learn to use the left. Indeed, it has been found that in left-handed persons suffering with aphasia the inferior frontal convolution affected is situ-

<sup>1</sup> Archives de Médecine, 1825.

<sup>2</sup> Bulletin de la société anatomique, tome iv. 1861.

<sup>5</sup> Op. cit., p. 274.

<sup>2</sup> Gazette hebdomadaire, April, 1865.

<sup>4</sup> London Hospital Reports, vol. i.



ated in the right hemisphere instead of the left hemispheres as is usually the case. By the same methods made use of in determining the functions of the convolutions about the fissure of Rolando, the angular gyrus, the inferior frontal convolution, etc., the functions of the remaining convolutions have been more or less satisfactorily made out, and may be resumed according to Ferrier,<sup>1</sup> as follows (Fig. 420):

1. Postero-parietal lobule: movement of the hind foot, as in walking.  
 2, 3, 4. Convolutions bounding the fissure of Rolando: movements of the arm and leg, as in climbing, swimming, etc.

5. Posterior extremity of the superior frontal convolution: extension forward of the arm and hand.

6. Anterior central convolution: supination and flexion of the forearm through action of biceps.

7, 8. Anterior central convolution: elevation and depression of the angle of the mouth, respectively.

9, 10. Inferior or third frontal convolution: movements of the lips and tongue, as in articulation, disease of which causes aphasia.

11. Posterior central convolution: retraction of the angle of the mouth.

a, b, c, d. Posterior central convolution: movements of the hand and wrist, as in clinching the fist.

12. Superior and middle frontal convolutions: lateral movements of the head and eyes, elevation of the eyelids, and dilatation of the pupil.

13, 13'. Supramarginal lobule, angular gyrus: centre of vision.

14. Superior temporo-sphenoidal convolution: centre of hearing.

V. Subiculum cornu ammonis: centres of smell, taste, etc.

H. Hippocampal region: centre of touch.

O. Occipital lobes: centres of organic sensations, hunger.

F. Frontal lobes: intellectual and reflective powers.

In concluding this necessarily brief account of the functions of the convolutions of the hemispheres, inasmuch as the surgeon at the present day may be called upon at any moment to trephine the skull and expose a particular convolution with the object of removing some morbid growth causing epileptiform convulsion, etc., the character of the latter indicating the convolution to be sought for, it may not appear superfluous if the general relations of the convolutions to the skull be pointed out. Taking certain easily recognized structures, such as the occipital protuberance, the parietal and frontal eminences, the external angular processes of the frontal bone, as landmarks, and making use further of the coronal, lambdoidal, and sagittal sutures, and by means of an imaginary line drawn from the squamosal suture vertically upward through the parietal eminence to the sagittal suture, the skull may be conceived as being mapped out into ten areas, within which may be found the most important of the fissures and convolutions.

The brain, like every other organ in the body, from time to time must rest, not only that the waste incidental to its functional activity may be repaired, but that its cells or whatever other structural elements may be concerned in the elaboration of consciousness may not be overtaxed,

<sup>1</sup> Op. cit., p. 305.

worn out by constant activity. This need of rest is especially manifest in the case of the brain, for no work is so exhausting as brain work, and when once the brain is fagged, worn out, nothing is so difficult as to restore to it its natural, healthy activity. This necessity of periods of rest rhythmically alternating with those of activity, is undoubtedly the underlying cause of sleep—"Tired nature's sweet restorer, balmy sleep"—however the latter may be brought about, and concerning which there still prevails considerable difference of opinion among physiologists. Thus it is held by Sommer<sup>1</sup> that as oxygen appears to be gradually stored up during sleep, as shown by the experiments of Pettenkofer, after a time it will have accumulated in such an amount as to accelerate materially the nutritive changes going on in the brain, etc., the effect of which is that awakening occurs. On the other hand, during the waking state this store of oxygen is gradually used up, as shown by increase in the amount of carbonic acid eliminated, the consequence of which is that exhaustion and general relaxation are experienced, followed by a desire to sleep. According to Pflüger,<sup>2</sup> the combination of this intramolecular oxygen with the carbon of the brain tissue is so violent as to amount to an explosion, which, taking place at successive intervals, maintains the brain in a waking condition; as the stored-up oxygen, however, is gradually used up the explosions diminish in frequency and violence until they cease altogether, and as a consequence sleep follows. A very plausible theory of the causation of sleep is that advanced by Dr. Cappie,<sup>3</sup> who holds that the molecular activity of the cerebral cells is diminished through less blood being supplied to them by the capillaries, and that consequently the brain occupies less space. But inasmuch as the brain-case must be full, the veins of the pia mater become proportionally distended, the effect of which is that although the absolute quantity of blood, and consequently the pressure, remains the same, the direction of the pressure is modified, being less from within and more on the surface of the brain, the latter or the altered direction of the pressure giving rise to sleep. This view is confirmed by the researches of Durham,<sup>4</sup> by whom it was shown that the brain during sleep is in an essentially bloodless condition, that not only the quantity of the blood but the velocity of its flow is diminished, and also by the observations of Dr. Hughlings Jackson,<sup>5</sup> who showed by ophthalmoscopic examination that the optic disk during sleep was whiter, the arteries smaller, the veins larger and the adjacent parts of the retina more anæmic than during the waking state. The amount of sleep required is affected by so many conditions, such as age, temperament, habit, mental and physical exhaustion, that it is absurd to lay down any rule upon the subject. In this respect, as in all others, physiological nature is our best guide. Go to bed when you feel sleepy and rise up when you awake. The mere fact that some individuals get along with only four or five hours' sleep without their health being affected is no argument whatever that such a small amount of sleep is only required and should suffice for every one. No greater mistake is made, and that so often, by students of medicine,

<sup>1</sup> Zeits. f. Rat. Med., Band xxxii. S. 214, 1868.

<sup>3</sup> The Causation of Sleep, Edinburgh, 1882.

<sup>5</sup> Royal London Ophth. Hosp. Reports.

<sup>2</sup> Archiv, 1875, S. 468.

<sup>4</sup> Guy's Hospital Reports, 31 ser. vol. vi.



physicians, and literary men generally, than to rob themselves of their natural sleep, with the laudable desire, it is true, of distinguishing themselves, but, unfortunately, at the cost of broken-down health and lost spirits, too often never to be regained.

Resuming what has been said of the functions of the cerebro-spinal axis in man, it may be stated in general that the spinal cord and medulla oblongata are the seat of excito-motor actions, the functions of the medulla differing from those of the cord rather in degree than in kind, the rhythmical performance of such complex functions as deglutition, circulation, and respiration, depending upon the medulla, from the fact of the nerves distributed to the tongue, fauces, larynx, heart, and lungs emanating from that portion of the spinal axis; that the pons Varolii, being that portion of the encephalon in which external impressions first become conscious ones, is the seat of excito-sensori-motor actions, as are also the basal ganglia, the corpora striata and thalami, being the centres of motion and sensation, respectively, the optic lobes the centres of vision; that the cerebellum is a reflex centre for the maintenance of equilibrium and coördination of locomotion; that the cerebral hemispheres, being the portion of the encephalon in which perceptions, ideas, emotions, and volition are developed, are the seat of excito-sensori-ideo-motor actions. It will be observed that up to the present moment, in our exposition of the functions of the encephalon, we have endeavored to offer only what appears to us to be well-established anatomical and physiological facts, merely mentioning, or not referring at all, to the remaining portions of the encephalon, whose functions have not as yet been made out—to describe simply the physical substratum of consciousness. It is needless to say, however, that whether or no the different parts of the encephalon and the different convolutions of the hemispheres really possess the functions assigned to them, that the phenomenon of consciousness is thereby in no wise explained. Admitting, for example, that the optic lobe is the centre of the sensation of sight, and that the exact nature of the molecular changes occurring in its cells when the sensation of sight is experienced were understood, we would be still unable to understand how the vibrations of light falling upon the retina give rise to visual sensations—that is, the manner in which a physical impression becomes a conscious sensation. In the present state, at least, of the development of our consciousness it appears impossible even to conceive of how the gap between matter and mind, the objective and subjective, can ever be bridged over. At all events, the phenomenon of consciousness can never be explained by a purely physiological investigation. We can say that the brain is the organ of the mind, even that it converts heat into thought, but, as viewed subjectively, the functions of the brain are synonymous with mental operations. The phenomenon of consciousness must be studied, not only objectively by the physiologist, but subjectively by the psychologist; nevertheless, too much stress must not be laid upon the distinction of matter and mind, of object and subject, as made by the metaphysician, since the existence of matter or mind, as shown by ultimate analysis, is only an inference. We are conscious of the sensations of color, hardness, roundness, weight, extension, etc., and we infer the

existence of something underlying these qualities, which we call matter, and which produces in us these sensations. We are directly conscious of these sensations, not of the matter supposed to cause them. The existence of matter being, therefore, an inference from our consciousness, it is impossible to say, not knowing anything whatever about its nature, whether it is akin to mind or not. On the other hand, suppose that matter does exist, it is certain that the various modes of motion ordinarily known as heat, light, sound, etc., are transformable in us into equivalent modes of consciousness, and we infer from these modes of motion the existence of something, the mind underlying these modes of consciousness, but of whose nature we know just as little as that of the matter, from the effects of which its existence is inferred. The idealist may argue that there is no such thing as matter apart from mind, since material forces are only cognizable as modes of consciousness, and the materialist may argue that there is no mind apart from matter, that the modes of consciousness are material, since what exists in us as consciousness is transformable into modes of motion, but it is evident that the forces of the inner are correlated with those of the outer world, the forces of the outer with those of the inner world, that if we begin with mind we end with matter, if with matter we end in mind; matter and mind being merely symbols of the unknown reality underlying both.



## CHAPTER XLV.

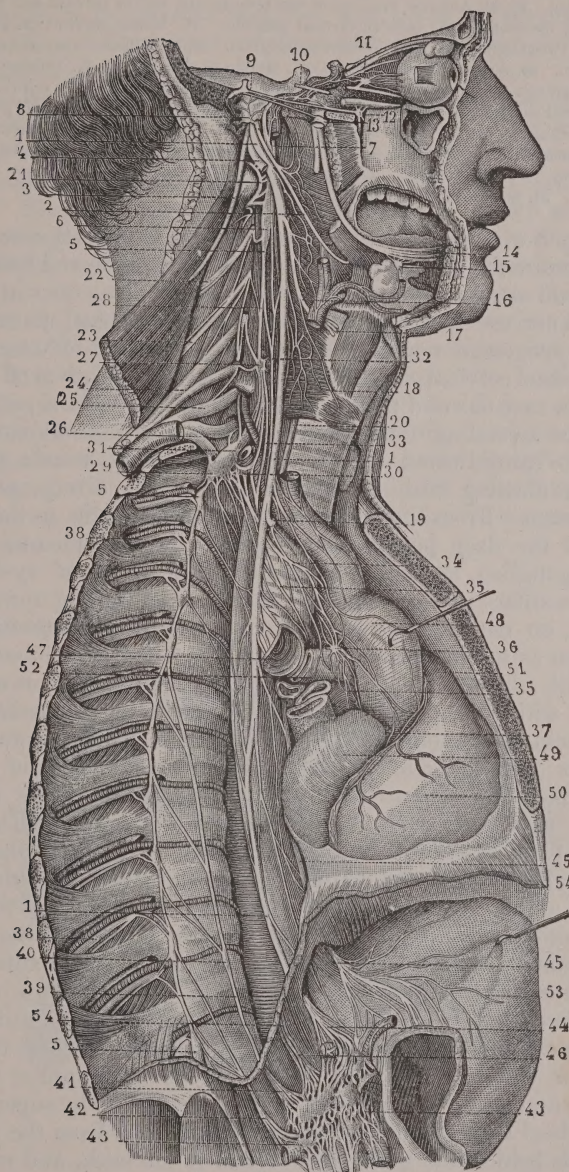
### SYMPATHETIC NERVOUS SYSTEM.

THE sympathetic system of nerves, or the system of organic vegetative life, also known as the trisplanchnic nerve, great intercostal nerve, etc., consists of a double chain of symmetrically disposed ganglia extending the entire length of the vertebral column, which, gradually converging, terminates finally as a single ganglion, the ganglion impar, resting upon the coccyx. While there is no doubt as to the manner in which the double ganglionated cord of which the sympathetic consists ends, it has not as yet been made out exactly how it begins; the observation of Ribes<sup>1</sup> that it begins as it ends, in a ganglion impar situated upon the anterior communicating artery, not having been confirmed by other anatomists. It may be mentioned, however, in this connection, that the author in dissecting various genera of monkeys, in more than one instance found such a ganglion, though he has failed, like others, to find it in man. Intercommunicating with the nerves of the cerebro-spinal system, and giving off during its course numerous branches forming intricate plexuses, such as the cardiac, solar, and hypogastric, the sympathetic nerves, as a general rule, follow the course of the great bloodvessels, entwining the latter as the ivy the oak, to supply the viscera of the great cavities of the body, etc.

The nerves of the sympathetic system are usually much smaller, softer, and less distinctly seen than those of the cerebro-spinal system, present a grayish aspect, and adhere closely, by connective tissue, to contiguous structures. While consisting of medullated nerve fibres, they are largely composed of the pale gray, gelatinous fibres of Remak, the latter resembling embryonic nerve fibres and the nerve fibres developed in the reunion of nerves. The ganglia of the sympathetic, whether of the ganglionated cord or its branches, do not differ essentially in structure from the ganglia of the posterior roots of the spinal nerves, large root of the fifth, trigeminal, glosso-pharyngeal, pneumogastric, etc. They consist of a mass of nerve cells smaller than those of the spinal ganglia, imbedded in a stroma of connective tissue, which is traversed by nerve fibres, the whole being enclosed by a tightly adherent membrane continuous with the sheath of the nerves upon which the ganglia occur, the latter looking like so many grayish-white or reddish-gray swellings or knots. The main ganglia and branches of the sympathetic being situated in the cervical, thoracic, abdominal, and pelvic regions, we may begin in our necessarily brief account of the physiological relation of the parts involved with the ganglia of the cervical region, and first with the superior cervical ganglion (Fig. 423).

<sup>1</sup> Mem. de la Soc. Med. d'Emulation, tome viii. p. 606.

FIG. 423.



Cervical and thoracic portion of the sympathetic. 1, 1, 1. Right pneumogastric. 2. Glosso-pharyngeal. 3. Spinal accessory. 4. Divided trunk of the sublingual. 5, 5, 5. Chain of ganglia of the sympathetic. 6. Superior cervical ganglion. 7. Branches from this ganglion to the carotid. 8. Nerve of Jacobson. 9. Two filaments from the facial, one to the sphenopalatine and the other to the otic ganglion. 10. Motor oculi externus. 11. Ophthalmic ganglion, receiving a motor filament from the motor oculi communis and a sensory filament from the nasal branch of the fifth. 12. Sphenopalatine ganglion. 13. Otic ganglion. 14. Lingual branch of the fifth nerve. 15. Submaxillary ganglion. 16, 17. Superior laryngeal nerve. 18. External laryngeal nerve. 19, 20. Recurrent laryngeal nerve. 21, 22, 23. Anterior branches of the upper four cervical nerves, sending filaments to the superior cervical sympathetic gan-



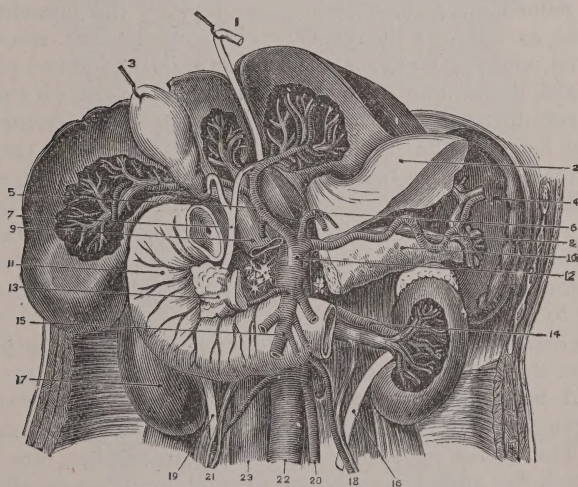
gion. 24. Anterior branches of the fifth and sixth cervical nerves, sending filaments to the middle cervical ganglion. 25, 26. Anterior branches of the seventh and eighth cervical and the first dorsal nerves, sending filaments to the inferior cervical ganglion. 27. Middle cervical ganglion. 28. Cord connecting the two ganglia. 29. Inferior cervical ganglion. 30, 31. Filaments connecting this with the middle ganglion. 32. Superior cardiac nerve. 33. Middle cardiac nerve. 34. Inferior cardiac nerve. 35, 35. Cardiac plexus. 36. Ganglion of the cardiac plexus. 37. Nerve following the right coronary artery. 38, 38. Intercostal nerves, with their two filaments of communication with the thoracic ganglia. 39, 40, 41. Great splanchnic nerve. 42. Lesser splanchnic nerve. 43, 43. Solar plexus. 44. Left pneumogastric. 45. Right pneumogastric. 46. Lower end of the phrenic nerve. 47. Section of the right bronchus. 48. Arch of the aorta. 49. Right auricle. 50. Right ventricle. 51, 52. Pulmonary artery. 53. Right half of the stomach. 54. Section of the diaphragm. (SAPPEY.)

The superior or first cervical ganglion, lying upon the rectus major muscle opposite the second and third cervical vertebræ and behind the internal carotid artery, is connected by intervening filaments with the upper four spinal nerves—the ganglia of the glosso-pharyngeal, pneumogastric, and the hypoglossal nerves. In addition to its cord of communication with the second cervical ganglion, the superior cervical gives off an ascending branch, vascular and pharyngeal branches, and the superior cardiac nerve. The ascending branch accompanying the internal carotid artery through the carotid canal divides into two branches, which, subdividing and communicating with each other around the artery, so form the carotid plexus. From the latter are given off filaments to the abducens nerve, and the deep petrosal which passes to the sphenopalatine, or Meckel's ganglion, the latter connected with the spinal system by the superior maxillary and great petrosal nerve. Continuing upward around the artery, on reaching the cavernous sinus, the sympathetic plexus is then known as the cavernous plexus, an important one, since it communicates with the semilunar ganglion and ophthalmic branch of the trigeminal with the ophthalmic ganglion, the latter connected with the spinal system by the ophthalmic and oculo-motor nerves, and with the oculo-motor and pathetic nerves. From the carotid and cavernous plexuses fine filaments are also given off which entwine themselves around all the branches of the internal carotid artery. The vascular branches of the superior cervical ganglion form plexuses upon the internal carotid artery and its branches. By the plexuses on the internal, maxillary, and facial arteries the sympathetic communicates with the otic and submaxillary ganglia respectively, the otic ganglion being connected with the spinal system by the small petrosal, the submaxillary ganglia by the chorda tympani. The pharyngeal branches, two or three in number, descending to the side of the pharynx, together with branches from the glosso-pharyngeal and pneumogastric nerves, form the pharyngeal plexus, which, as we have already mentioned, supplies the mucous membrane and constrictor muscles of the pharynx. The superior cardiac nerve, derived from the first cervical ganglion and from the cord below it, descends behind the great bloodvessels of the neck, and entering the thorax passes on the right side either in front of or behind the subclavian artery, thence along the innominate to the back of the arch of the aorta, to end in the cardiac plexus. On the left side of the nerve follows the carotid artery in its course to the cardiac plexus.

The superior cardiac nerve communicates with the pneumogastric, and gives off filaments to the inferior thyroid artery. The middle, or second cervical ganglion, resting upon the inferior thyroid artery, and

situated opposite the fifth cervical vertebra, is connected with the third cervical ganglion by several branches, and gives off filaments to the fifth and sixth spinal nerves, branches which follow the inferior thyroid artery to the thyroid body, and the middle cardiac nerve. The latter, as it descends the neck, receives filaments from the superior and inferior cardiac and pneumogastric nerve, and ends in the cardiac plexus. Occasionally the middle cervical ganglion is indistinct, or even absent; in such cases it appears to be fused with the inferior or third cervical ganglion. The latter, situated behind the vertebral artery and between the transverse process of the last cervical vertebra and the first rib, gives off, in addition to the branches going to the first thoracic ganglion, branches to the seventh and eighth spinal nerves, to the vertebral artery, and the inferior cardiac nerve, which, after receiving filaments from the middle cardiac and inferior laryngeal nerves, and sometimes from the first thoracic ganglion, terminates in the cardiac plexus. Occasionally the inferior cardiac nerve of the left side becomes blended with the middle cardiac nerve. The three cardiac and pneumogastric nerves, together with branches from the first thoracic ganglion, form the cardiac plexus. The latter, situated behind and beneath the arch of the aorta, gives off branches which, accompanying the coronary arteries, constitute the coronary plexuses.

FIG. 424.



Solar plexus. (HIRSCHFELD.)

While the cervical portion of the sympathetic consists, as we have seen, of three ganglia, etc., the thoracic portion consists of usually twelve ganglia, resting upon the heads of the ribs, and covered by the pleura. The first thoracic ganglion, as already mentioned, is connected with the last cervical, and the last thoracic with the first lumbar, the connecting cord of the latter passing through the diaphragm. Each thoracic ganglion usually gives off two narrow cords, the rami commu-



nicantes, which pass to the nearest intercostal nerve. The upper six thoracic ganglia give off, also, branches to the aorta, intercostal blood-vessels, and the œsophageal and pulmonary plexuses of the pneumogastric nerve. The lower six thoracic ganglia give off, in addition to the branches going to the aorta, branches which go to form the three splanchnic nerves. The great splanchnic nerve, deriving its roots from the sixth to the tenth thoracic ganglia, inclusive, perforates the crus of the diaphragm, and terminates in the semilunar ganglion. The small splanchnic nerve, deriving its roots from the tenth and eleventh thoracic ganglia, passes through the diaphragm with the preceding nerve, and terminates in the solar plexus. The third splanchnic, sometimes absent, coming from the twelfth thoracic ganglion, pierces the diaphragm, and terminates in the renal plexus.

The solar plexus (Fig. 424), so called on account of the numerous filaments radiating from it, is situated behind the stomach and in front of the aorta and crura of the diaphragm, and surrounding the coeliac and commencement of the superior mesenteric artery, extends to between the suprarenal bodies. It consists of an intricate mixture of nerves and ganglia; among the former may be mentioned the great and small splanchnics, as well as filaments from the pneumogastric nerve; among the latter the semilunar ganglion (Fig. 425), so called on account of its being situated on each side of the plexus, at the side of the coeliac and superior mesenteric arteries. From the solar plexus emanate numerous plexuses, named after the vessels around which the branches entwine themselves, as follows: the phrenic, coronary, hepatic, splenic, suprarenal, renal, and spermatic, superior mesenteric, and aortic plexus. The aortic plexus, descending upon the aorta from the solar plexus, of which it is the continuation, after giving off the inferior mesenteric plexus terminates below in the hypogastric plexus. The latter very intricate plexus, situated between the common iliac bloodvessels, extends downward as the inferior hypogastric plexuses on each side of the rectum, and after receiving branches from the lower lumbar and sacral ganglia, the lower two or three sacral nerves, and the inferior mesenteric plexus, gives off the vesico-prostatic, or the vesico-vaginal and uterine plexuses, according to the sex respectively.

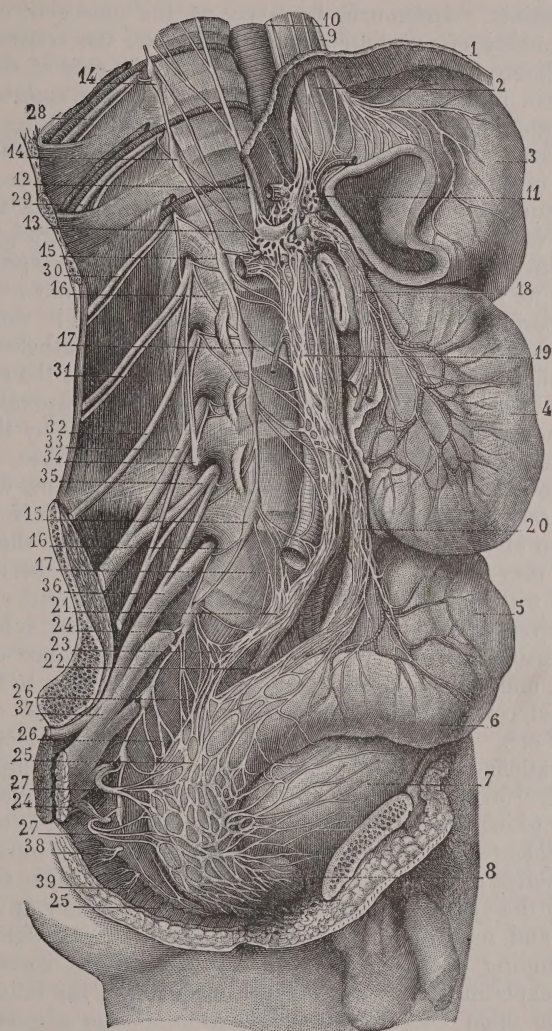
The lumbar portion of the sympathetic consists of four or five ganglia situated at the sides of the vertebræ which communicate with each other, and with the adjacent lumbar nerves, as in the case of the thoracic ganglia, and give off branches to the aortic and hypogastric plexus. The sacral ganglia, usually four in number, are connected likewise with the spinal nerves, and give off branches to the hypogastric plexus. As already mentioned, the single coccygeal ganglion or ganglion impar, with connections similar to those of the sacral ganglia, is common to the two sympathetic nerves. While considerable difference of opinion prevailed at one time as to whether the ganglia of the sympathetic were sensitive, there is no doubt on this point at present; mechanical or chemical irritation of the thoracic or semilunar ganglia in dogs, calves, and rabbits, having been shown by Flourens,<sup>1</sup> Brachet,<sup>2</sup>

<sup>1</sup> Recherches expérimentales sur les propriétés et les fonctions du système nerveux. p. 230. Paris, 1842.

<sup>2</sup> Recherches expérimentales sur les fonctions du système ganglionnaire, p. 305. Bruxelles, 1834.

Muller,<sup>1</sup> Longet,<sup>2</sup> etc., to give rise to pain. The sensibility of the sympathetic, however, is far from acute, being indeed, dull, as com-

FIG. 425.



Lumbar and sacral portions of the sympathetic. 1. Section of the diaphragm. 2. Lower end of the oesophagus. 3. Left half of the stomach. 4. Small intestine. 5. Sigmoid flexure of the colon. 6. Rectum. 7. Bladder. 8. Prostate. 9. Lower end of the left pneumogastric. 10. Lower end of the right pneumogastric. 11. Solar plexus. 12. Lower end of the great splanchnic nerve. 13. Lower end of the lesser splanchnic nerve. 14, 14. Last two thoracic ganglia. 15, 15. The four lumbar ganglia. 16, 16, 17, 17. Branches from the lumbar ganglia. 18. Superior mesenteric plexus. 19, 21, 22, 23. Aortic lumbar plexus. 20. Inferior mesenteric plexus. 24, 24. Sacral portion of the sympathetic. 25, 25, 26, 26, 27, 27. Hypogastric plexus. 28, 29, 30. Tenth, eleventh, and twelfth dorsal nerves. 31, 32, 33, 34, 35, 36, 37, 38, 39. Lumbar and sacral nerves. (SAPPEY.)

<sup>1</sup> Muller : Physiology, vol. i. p. 712. London, 1840.    <sup>2</sup> Physiologie, tome iii. p. 593. Paris, 1869.



pared with that of the cerebro-spinal system. As regards the excitability of the sympathetic, it has also been shown by Muller,<sup>1</sup> Longet,<sup>2</sup> and others, that stimulation of the ganglia, splanchnic nerves, etc., by electricity or chemical irritants causes contractions of the muscular coat of the intestines. Inasmuch, however, as the muscular coat of the intestine consists of unstriated muscular tissue, the contraction does not immediately follow the stimulation, as in the case of the cerebro-spinal system and striated muscle, and further, the contraction lasts longer, another characteristic of the effect of stimulating unstriated muscular tissue. Since, however, the most important effects following stimulation of the sympathetic can be obtained, as we shall see presently, by the stimulating of the cerebro-spinal system, and as the ganglia and fibres of the sympathetic lose their properties through atrophy, degeneration, etc., when separated from the cerebro-spinal system, with which we have just seen they are invariably connected, as shown by the experiments of Bernard,<sup>3</sup> Courvoisier,<sup>4</sup> etc., it would appear that whatever properties are possessed by the sympathetic are due to its connections with the cerebro-spinal system. That the sympathetic system, in fact, is only an appendage of the cerebro-spinal system, is not only shown by the facts just referred to, but also by the very important one in this connection that in the lowest fishes, amphioxus, myxine, the sympathetic system is undeveloped or absent, which would not be the case were its presence an indispensable element in the nervous organization of a vertebrate. Up to the beginning of the eighteenth century it may be said that absolutely nothing had been definitely established with regard to the functions of the sympathetic system. In 1712, however, Pourfour du Petit<sup>5</sup> divided the cervical sympathetic in a dog, repeating the experiment in 1725, in the presence of Winslow and Senac, and called attention among its consequences to the redness and injected condition of the conjunctiva, the contracted condition of the pupil,<sup>6</sup> etc. The conclusion drawn by Petit from his experiments and observations was that the intercostal nerve, as the sympathetic was then called, "furnished spirits to the conjunctiva, to the glands, and to the vessels which are found in these parts, the relaxation of the parts being so evident that there almost always ensues a slight inflammation of the conjunctiva due to the swelling of the vessels;" that the influence exerted by the sympathetic was propagated from below upward toward the brain, and not from the brain downward, as was often supposed. Notwithstanding the importance of the conclusions correctly drawn from his experiments by Petit with reference to the influence of the sympathetic upon the circulation, nutrition of the eye, etc., nearly a century passed without anything further being added to our knowledge of the functions of the sympathetic. In 1812, however, Dupuy, of Alfort, having removed the superior cervical ganglion in horses, called attention among the effects of the experiment, particularly to the in-

<sup>1</sup> Op. cit., p. 713.

<sup>2</sup> Op. cit., p. 595. *Système Nerveux*, tome ii. p. 568. Paris, 1842.

<sup>3</sup> *Journal de la physiologie*, tome v. p. 407. Paris, 1862.

<sup>4</sup> *Archiv of Micros. Anat.*, Band ii. S. 30. Bonn, 1886.

<sup>5</sup> *Mémoires de l'Acad. des Sciences*, p. 1. Paris, 1727.

<sup>6</sup> Due to the unopposed action of the third pair of nerves supplying the circular muscular fibres of the iris.

jected condition of the ocular conjunctiva, and to the elevation of temperature in the ears, head, and neck, which were bathed in sweat; the general conclusion arrived at by Dupuy<sup>1</sup> being that the sympathetic exercises a great influence on the nutritive functions. While Petit described the effects of cutting the cervical sympathetic, and Dupuy of removing the superior cervical ganglion neither of these experimenters offered any definite explanation of the hyperæmia noted in both cases, nor Dupuy of the rise in temperature in the latter one. Indeed, the true explanation of the phenomena at that period would have been impossible, the structure of the arteries not yet being understood.

Even though Valentin<sup>2</sup> had shown, in 1839, that the arteries contracted in response to stimulation of the nerves distributed to them, it was not admitted that the middle coat of the arteries contained muscular fibres until 1840, when such was actually demonstrated to be the case beyond doubt by Henle.<sup>3</sup> During the same year, Stirling,<sup>4</sup> like Henle, was led to the conclusion that there existed nerves comparable to those distributed to the muscles generally, which act upon the blood-vessels, either directly or reflexly, and which he called "vasomotor nerves." In 1852 Brown-Séquard<sup>5</sup> divided the cervical sympathetic on one side in rabbits, and called attention, as Bernard<sup>6</sup> had done in the previous year, to the hyperæmia and elevation of temperature, often amounting to as much as 11° F. on the corresponding side of the head and ear, and for the first time gave the true explanation of the phenomena in attributing the rise in temperature of the parts affected to the supply of blood being increased through the dilatation of the blood-vessels, and by showing that while section of the sympathetic in paralyzing the muscular coats of the arteries permits of their dilatation, electrical stimulation of the central cut end of the sympathetic causes their contraction again, and with the latter the restoration of the parts to their normal condition. To Brown-Séquard must be accorded, therefore, the discovery, not exactly of vaso-motor nerves, since the existence of such had been previously indicated by Henle and Stirling, but of the vasomotor, or, more especially, of the vaso-constrictor nerves of the cervical sympathetic, and of their mode of action in influencing the temperature, etc., of the parts to which the latter are distributed. It should be mentioned, however, in justice to Bernard, that three months after Brown-Séquard's discovery, and without being aware of it, Bernard<sup>7</sup> offered the same explanation of the experiments performed by him during the previous year (1851), but at that time by him incorrectly interpreted. The vaso-motor, or vaso-constrictor nerves, as we shall hereafter call them, since, through their constricting effect upon the muscular coat of the bloodvessels, the normal calibre of the latter are maintained, and the tissues supplied with the proper amount of blood, are found, not only in the cervical, but also in the thoracic and

<sup>1</sup> Journal de Convisart et Leroux, 1816, tome xxxvii, p. 340. Mechel's Archiv, 1818, Band iv. S. 105.

<sup>2</sup> De Functionibus Nervorum Cerebraliū et Nervi Sympathetici, p. 153. Bernæ, 1839.

<sup>3</sup> Wochenschrift für die gesammte Heilkunde, 1840, No. 29, S. 329.

<sup>4</sup> Recherches path. et med. pratiques sur l'irritation. Leipzig, 1840.

<sup>5</sup> The Medical Examiner, New Series, vol. viii. p. 489. Philadelphia, August, 1852.

<sup>6</sup> Comptes rendus de la société de biologie, tome iii. p. 163. Paris, 1851.

Ibid., 1852, tome iv. p. 169.



abdominal portions of the sympathetic and in the brachial and sciatic plexuses, supplying the upper and lower extremities. While the vaso-constrictor nerves are apparently given off as fibres from the sympathetic ganglia, in reality they are derived, as shown by recent investigation,<sup>1</sup> from the spinal cord, since division or stimulation of the latter, or of certain spinal nerves in certain definite regions, is followed by dilatations or contractions of the bloodvessels, just as if the vaso-constrictor nerves had themselves been divided or stimulated. Thus, for example, while the vaso-constrictor nerves of the head are apparently derived from the superior cervical ganglion, they can be traced by their division and electrical stimulation through the cervical cord of the sympathetic to the anterior roots of the first three dorsal spinal nerves, and thence into the anterior columns of the cord. Further, according to Bernard,<sup>2</sup> whilst the fibres distributed to the dilating muscular fibres of the iris, thereby causing dilatation of the pupil, are derived from the first two dorsal nerves (cilio-spinal centre), those distributed and influencing the calibre of the bloodvessels are derived from the third dorsal nerve. In the same manner, the vaso-constrictor nerves supplying the bloodvessels of the upper extremity, while apparently emanating from the first thoracic ganglion, are, in reality, derived from the spinal cord, passing off from the latter with the anterior roots of the third to the seventh dorsal nerves inclusive, and thence traversing the thoracic portion of the sympathetic and the inferior thoracic ganglion, reach the brachial plexus by the rami communicantes, to be finally distributed with the branches of the plexus, while such of the vaso-constrictor nerves as are derived from the plexus itself are given off with the anterior roots of the cervical nerves. The vaso-constrictor nerves supplying the bloodvessels of the abdominal viscera, more especially the splanchnic nerves, are largely derived from the dorsal and lumbar portion of the cord; the latter, together with the sacral portion of the cord, giving off fibres which pass through the lumbar and sacral plexuses to the sympathetic, and thence into the lower extremities, supplying the bloodvessels of the latter. Inasmuch, then, as the vaso-constrictor nerves are derived from the spinal cord, traversing more particularly its anterior columns, it might naturally be supposed that all these nerve fibres at some point of the cord, the upper portion most probably, would be brought to a focus, so to speak, and that stimulation of such a portion of the cord would cause all of the bloodvessels to contract, and a corresponding rise in blood pressure and division of the same, a dilatation of the vessels and fall in blood pressure.

Such a focus or vaso-motor centre has indeed been found in animals, not exactly by anatomical demonstration, but by means of successive sections of the cord below upward, and from above downward, and localized in the rabbit, for example, by Owsjanikow<sup>3</sup> in the floor of the fourth ventricle on either side of the middle line just one millimetre behind the optic lobes, and between four and five millimetres in front of

<sup>1</sup> Budge and Waller: *Comptes Rendus*, tome xxxiii. p. 372. Paris, 1851. Ludwig and Thiry: *Wiener Sitzungsberichte*, 1861, Band xlix. II. Abtheilung, S. 421. Vulpian: *Leçons sur l'Appareil vaso-moteur*, p. 189. Paris, 1875.

<sup>2</sup> *Comptes Rendus*, tome iv. p. 383.

<sup>3</sup> Ludwig's *Arbeiten*, 1871, S. 210.

the nib of the calamus scriptorius. From this centre emanate impulses, which transmitted through the anterior columns of the cord and anterior roots of the spinal nerves pass thence to the sympathetic ganglia and vaso-constrictor nerves, and through the latter maintain the normal calibre of the vessels or the vascular tonus. Inasmuch as the muscular fibres of the middle coat of the bloodvessels is disposed in a circular manner at right angles to the long axis of the vessel, it is not difficult to understand why stimulation of the vaso-constrictor nerves is followed by contraction of the vessels—indeed, the disposition of the nervous and muscular fibres being such, it can hardly be conceived how it should be otherwise, and yet, strange as it may appear, as first shown by Bernard<sup>1</sup>, there are also nerves the stimulation of which causes dilatation of the bloodvessels instead of contraction, and which may therefore be called vaso-dilator nerves; among such may be mentioned the chorda tympani, the auriculo-temporal, the nervi-erigentes of the penis; stimulation of these nerves causing dilatation of the vessels of the tongue,<sup>2</sup> of the ear, and of the corpora cavernosa of the penis,<sup>3</sup> respectively. Though numerous explanations have been offered of the manner in which the vaso-dilator nerves act, it must be admitted that none of them are satisfactory, and that it is not yet understood how their stimulation causes dilatation of the bloodvessels. Thus, it has been said that the stimulation of a vaso-dilator nerve causes the vein of the part to contract, and that in consequence an obstacle is offered to the passage of the blood from the artery to the capillary, which is the cause of the dilatation of the artery. As a matter of fact, however, the vein does not contract, but dilates as much as the artery. It has also been suggested that the stimulation of a vaso-dilator nerve excites the activity of the anatomical elements of the part to which the nerve is distributed, the effect of which in the case of a salivary gland, for example, would be that its secretory activity being increased more blood would flow to the part, and the vessels would dilate. Unfortunately, however, for this hypothesis, in the absence of all secretion, as in the case of an animal poisoned with atropine, the vessels of the tongue will still dilate if the chorda tympani be stimulated. Another explanation, a too common one when physiological phenomena remain unexplained, is that of inhibition, it being held that vaso-dilator nerves inhibit or paralyze the vaso-constrictor nerves. Apart, however, from the fact that the dilatation of an artery following stimulation of a vaso-dilator nerve is greater than that following paralysis of the vaso-constrictor nerve, to say that the one nerve inhibits the other is rather another way of stating the fact to be explained than an explanation of it. Whatever value may be attached to the explanations offered, whether they be accepted or not, nevertheless, there can be no question as to the fact of their being vaso-dilator as well as vaso-constrictor nerves, and that in all probability they emanate from a focus or centre close to the vaso-motor or constrictor one, already described, if not actually in the latter. The vaso-constrictor or vaso-

<sup>1</sup> Systeme Nerveux, tome ii. p. 144. Paris, 1858. Liquides de l'Organisme, tome i. p. 312.

<sup>2</sup> Vulpius, op cit., p. 158.

<sup>3</sup> Eckhard : Untersuchungen über die Erektion des Penis beim Hunde. Beiträge zur Anat. u. Phys. Abhand. vii. Giessen, 1862.



dilator nerves can be excited reflexly as well as directly. Thus, as first shown by Brown-Séquard<sup>1</sup> and Tholozan, if a thermometer be held in one hand and the other hand surrounded by ice or very cold water, in a very short time the temperature of the hand holding the thermometer will fall, the general temperature of the body, however, remaining unaffected, an effect which can only be explained on the supposition that the impression due to the cold is transmitted by the sensory nerves to the spinal cord and thence reflected by the vaso-constrictor nerves to the vessels of the hand holding the thermometer. For the same reason, according to Brown-Séquard,<sup>2</sup> if one foot be immersed in water at about 41° F., the temperature of the other foot will fall in a few minutes perhaps 7° F. It has also been shown by Vulpian<sup>3</sup> that if the sciatic nerve be divided, as in a dog, for example, and the central end stimulated, not only the vessels of the limb contract, but also almost all the vessels of the body, the under surface of the tongue even becoming pale through constriction of its vessels. The same reflex effect can also be induced by stimulation of almost any of the sensory nerves, of the posterior roots of the spinal nerves, and even by irritation of the skin. As illustrations of reflex vaso-dilator action may be mentioned, the dilatation of the internal saphenous artery following stimulation of the central cut end of the dorsal nerve of the foot, and the dilatation of the vessels of the ear, brought about through excitation of the central end of the auriculo-temporal nerve, or through stimulation of the central end of the sciatic nerve.

While the functions that we have attributed to the sympathetic nerve are those possessed by that of animals, there is no doubt that the functions of the sympathetic in man are essentially the same. The blush and pallor due to emotion are familiar examples of reflex vasomotor actions in man. A number of cases have been now recorded by J. W. Ogle,<sup>4</sup> Panas,<sup>5</sup> Verneuil,<sup>6</sup> Trelat,<sup>7</sup> Poiteau,<sup>8</sup> W. Ogle,<sup>9</sup> Bartholow,<sup>10</sup> Seeligmuller,<sup>11</sup> Nicati,<sup>12</sup> Eulenberg,<sup>13</sup> in which rise of temperature, unilateral sweating of the neck and head, hyperæmia of the conjunctiva, contraction of the pupil, were all observed more or less in consequence of paralysis of the sympathetic due to pressure exerted by aneurisms, tumors, etc., while, according to Vulpian,<sup>14</sup> lesions of the spinal cord may be localized from the vascular dilatation developed in the upper extremities as a consequence of the injury to the vasomotor nerves arising from it. It may be also mentioned in this connection that before most of these observations had been made, Wagner<sup>15</sup> had noticed that, in the case of a decapitated woman, powerful galvanization of the sympathetic caused dilatation of the pupil. While the scope of this work does not permit of a detailed account of the influence exerted

<sup>1</sup> Journal de Brown-Séquard, 1858, tome i. p. 497.

<sup>2</sup> Op. cit., p. 237.

<sup>3</sup> Mem. de la Soc. de Chirurgie, 1864, t. vi. p. 333.

<sup>4</sup> Bul. de la Soc. de Chirurgie, 1864, 2d série, t. v. p. 167

<sup>5</sup> Gaz. des hôpitaux, Paris, 2 Juin, 1868

<sup>6</sup> Med.-Chir. Trans., vol. lli, p. 150. London, 1869.

<sup>7</sup> Quarterly Journal of Psych. Medicine, vol. lii, p. 134. New York, 1869.

<sup>8</sup> Berlin klin. Wochenschrift, 1872, No. 2.

<sup>9</sup> La paralysie du nerf sympathétique. Lausanne, 1873.

<sup>10</sup> Berlin. klin. Wochenschrift, 1869, S. 287.

<sup>11</sup> Journal de physiologie, tome iii. p. 175. Paris, 1860.

<sup>12</sup> Ibid., p. 502.

<sup>13</sup> Med.-Chir. Trans., vol. xli. p. 397.

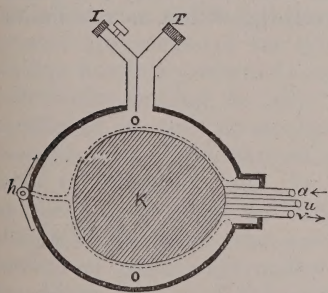
<sup>14</sup> Thèse de Paris, 1869, No. 2.

<sup>15</sup> Op. cit., p. 195.

by the sympathetic nervous system upon nutrition, it will have been seen, no doubt, from what has been already said, that its influence must be very great, since the amount of blood distributed to the stomach, intestine, liver, kidney, etc., is regulated by the vasomotor nerves. The reflex flow of the alimentary secretions in response to the excitement developed through the presence of food, their natural stimulus, the great vascularity of the liver, spleen, pancreas, during digestion, is brought about through the influence of the sympathetic nerves distributed to these organs. The rapidity and extent with which the absorption of the digested food takes place depends largely upon the condition of the portal circulation, as influenced by the vaso-motor nerves, and more particularly by the splanchnic. The circulation of the blood, as we have already seen, is modified by the combined effects of the depressor and vasomotor nerves. It is also through the intermediate action of the latter that the cerebro-spinal centres, more especially those of the medulla, as shown by Bernard<sup>1</sup> and Vulpian,<sup>2</sup> influence the biliary and glycogenic functions of the liver and the secretion of urine by the kidneys. That the amount of blood circulating through the latter, and therefore the amount of urine secreted, is influenced by the vaso-motor nerves, can be readily demonstrated by means of the oncometer and oncograph, by which the volume of the kidney in the living animal can be shown to vary with the blood circulating through it, the amount of the latter being regulated by the vasomotor nerves.

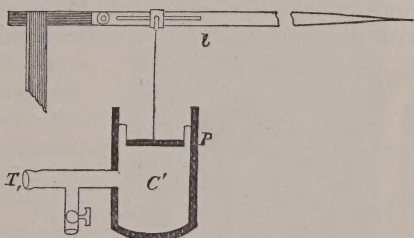
The oncometer (Fig. 426) is a metallic capsule, shaped like a kidney, composed of two halves moving on a hinge (*h*), by which the kidney is introduced, the renal vessels (*a, v, u*) passing out by the oppo-

FIG. 426.



Oncometer. K. Kidney; the thick line is the metallic capsule. *h*. Hinge. I. Tube for filling apparatus. T. Tube to connect with T<sub>1</sub>. *a, v, u*. Artery, vein, ureter. (STIRLING, after ROY.)

FIG. 427.



Oncograph. C' Chamber filled with oil, communicating by T<sub>1</sub> with T. *p*. Piston. *l*. Writing lever (STIRLING, after ROY.)

site opening, The kidney (K) is surrounded with a thin membrane, and the space (*o*) between the latter and

the inner surface of the capsule filled with warm oil introduced through the tube I, which can be closed with a stopcock. The tube T being adapted to the tube T<sub>1</sub> leading into the metallic chamber C' of the oncograph (Fig. 427), also filled with oil, any increase in the volume

<sup>1</sup> Systeme Nerveux, tome i. pp. 398-463. Physiologie Experimentale, tome i. p. 345.

<sup>2</sup> Op. cit., tome i. pp. 541, 556.



of the kidney will force the oil from the space *o* into the chamber *C'*, and the piston *p* will be elevated, and with it the recording pen. On the other hand, any diminution in the volume of the kidney through stimulation of the vaso-constrictor nerves will cause the oil to flow from *C'* into *o* and the piston, and with it the recording pen, will fall. By

FIG. 428.



adapting the pen to the cylinder we can get a trace of the so-called kidney curve (Fig. 428).

We have already seen that through the contractions and dilatations of the cutaneous bloodvessels the blood either remains in the deeper portions of the skin, or comes to the surface of the body, the heat produced in the body, in the one case being retained within it, and, in the other lost by either radiation, conduction, etc., and that the application of cold to the general surface so constricts the cutaneous bloodvessels that the blood does not rise to the surface, the heat thereby being retained, which would otherwise be lost. That this effect is due to the impression made by the cold being transmitted by the sensory nerves to the spinal cord, and thence reflected by the vaso-constrictor nerves to the cutaneous bloodvessels, is shown by the fact of a curarized hot-blooded animal losing this compensating power, through which the heat of the body is normally retained, even though the latter be exposed to cold, the temperature of the curarized animal not being a constant one, but, like that of the cold-blooded one, varying within narrow limits with the temperature of its surroundings.

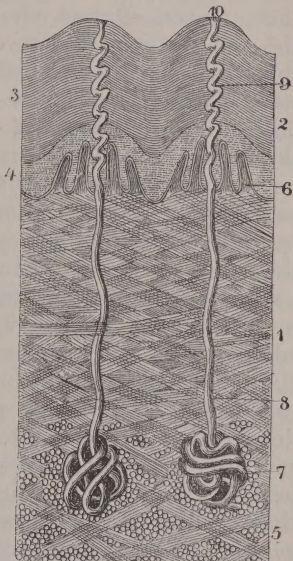
## CHAPTER XLVI.

### THE SKIN AND ITS APPENDAGES. PERSPIRATION. GENERAL AND TACTILE SENSIBILITY.

#### THE SKIN.

THE skin or integument constitutes a general protective and sensory covering for the surface of the body. In addition to these important functions, however, in eliminating the sweat, carbonic acid, urea, etc., the skin acts also as an excretory organ, supplementing, in this respect, the action of the lungs and kidneys. As we have already seen, the skin, too, in a great measure regulates the production and distribution of heat. To a certain extent, also, the skin acts as an absorbing surface. Further, through special modifications of its sensory structure, the skin is endowed with tactile sensibility, and thereby ministers to the sense of touch. The skin in addition, then, to being sensory and protective, possesses, as well, excretory, calorific, absorbing, and tactile functions. The general appearance of the skin, its extensibility, flexibility, elasticity, and color are sufficiently familiar to all. It may be mentioned in this connection, however, that the color of the skin in the different races of mankind, and the varieties of complexion observed in different individuals of the same race, are due to the amount of pigmentary matter present in the deeper layers of the epidermis, and that the color of the true skin, or dermis, is whitish and semi-transparent, its apparent pinkish color being due rather to that of underlying parts and the blood circulating through the latter. The furrows and folds of the skin are caused partly by the muscles and joints and partly by loss of elasticity in the skin itself, and by the deposition in it of fat. Faint, irregular lines are also observed on most parts of the surface of the skin, upon the palms of the hand and soles of the feet, and particularly upon the palmar surface of the last

FIG. 429.



Vertical section of the skin of the forefinger across two of the ridges of the surface, highly magnified. 1. Dermis composed of an intertexture of bundles of fibrous tissue. 2. Epidermis. 3. Its cuticle. 4. Its soft layer. 5. Subcutaneous connective and adipose tissue. 6. Tactile papillæ 7. Sweat glands. 8. Duct. 9. Spiral passage from the latter through the epidermis. 10. Termination of the passage on the summit of ridge. (LEIDY.)



phalanges; these lines are well marked in the latter situation, being disposed as concentric curves depending upon the regular arrangement of the underlying papillæ of the true skin or dermis. According to Sappey,<sup>1</sup> the cutaneous surface, on the average in man, is equal to about ten square feet, in woman from six to eight, though in men above the ordinary size it may amount in extent to from twelve to even eighteen square feet. The significance of such variations physiologically will become apparent presently when we consider the excretory functions of the skin.

In harmony with the protective functions of the skin, its thickness varies very much in different parts. Thus, where naturally exposed to constant pressure and friction, as on the soles of the feet or the palms of the hands, the skin, as we shall see, is much thicker than that of the face, eyelids, etc.

The skin consists of two layers, the dermis and epidermis, special modifications of the latter constituting the hair and nails, the sebaceous, mammary, and sweat glands. The dermis or true skin, also known as the cutis vera, corium, etc. (Fig. 429), constituting the deeper layer of the skin, is more or less closely connected to the underlying parts by the connective tissue of the adipose layer of the superficial fascia, or when the adipose layer is absent, by the loose connective tissue to the deeper layer of the fascia or subjacent structure, thereby allowing the skin a certain amount of movement backward and forward. The thickness of the adipose layer varies very much in different individuals and in different parts of the same individual. Thus while there is no fat beneath the skin of the eyelids, the upper and outer part of the ear, the penis, and the scrotum, a layer about the twelfth of an inch in thickness is usually present beneath the skin of the cranium, the nose, the neck, the knee and elbow, and the dorsum of the hand and foot; the adipose layer, on an average, in other situations, measuring from a sixth to one-half an inch. In fat persons, however, it may attain a thickness of one inch or even more. There is no well-defined line of demarcation between the dermis and the underlying adipose tissue, and after separating the two the dermis looks like a coarsely corded network, the meshes being occupied by small round masses of adipose tissue. The dermis consists principally of a dense intertexture of bundles of fibrous tissue crossing one another at acute angles in different directions, mingled with amorphous matter and some elastic tissue, the latter being most abundant on the front of the body and around the joints. It contains also unstriated muscular fibres which, passing downward from the more superficial part of the dermis are inserted into the hair follicles, and which, when excited to contract through the stimulus of cold, emotions of fear, or electricity, elevate the hairs and so give rise to the condition known as "goose flesh." In consequence of the gradual transition of the dermis into the subjacent tissues, its exact thickness is difficult to estimate. It may be said, however, to be about  $\frac{1}{72}$  of an inch thick on the eyelids, from the  $\frac{1}{48}$ th to  $\frac{1}{24}$ th of an inch on the front of the body, and from the  $\frac{1}{24}$ th to the  $\frac{1}{8}$ th of an inch on the back of the

<sup>1</sup> Anatomie, tome ii. p. 447. Paris, 1852.

body and the heels, being thickest where the entire skin presents that condition.

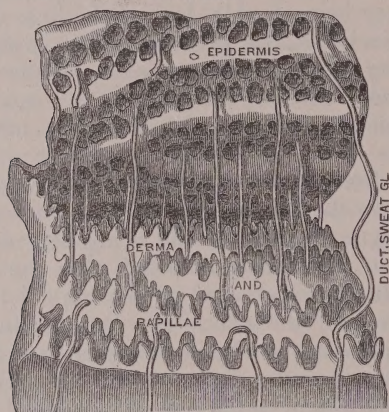
The dermis is thinner in the female than in the male, about half as thick in children as in adults, and becomes thinner in old age. At its outer surface the dermis is quite dense, being defined by a more homogeneous layer or basement membrane, and projects here and there as small eminences, the papillæ, into the deeper layers of the dermis. The papillæ on which the perfection of the skin as an organ of touch largely depends, they being highly developed where the sense of touch is exquisite, and *vice versa*, are of two kinds, simple and compound, the latter consisting of two, three, or more simple papillæ springing from a common base. The papillæ composed of a continuation of the fibrous and amorphous structure of the dermis and defined by the basement membrane of the latter vary in number and size in different parts of the body. They are most numerous and longest in the palms of the hands and soles of the feet, attaining in these situations a length of the  $\frac{1}{360}$ th to the  $\frac{1}{120}$ th of an inch, and being here disposed in double rows on the ridges of the dermis, of which they are the continuation, and give rise, as already mentioned, to the curved lines so noticeable on the palmar surfaces of the skin of the last phalanges of the fingers and toes. The papillæ are also quite numerous on the prepuce, glans penis, nymphæ, clitoris, and nipple. In other portions of the body they are less numerous and small, measuring only from the  $\frac{1}{360}$ th to the  $\frac{1}{960}$ th of an inch. In the face, for example, the papillæ are so little developed as to be hardly recognizable. Most of the papillæ of the palms, fingers, soles, toes, and nipples, especially the compound kind, contain tactile corpuscles in which, as already mentioned, the cutaneous nerves terminate. It will be remembered also that the digital nerves of the fingers and toes appear to terminate in similar shaped, though larger bodies, the Pacinian corpuscles, situated in the subcutaneous tissue, and the nerves supplying the skin of the glans penis and clitoris in the Krause corpuscles, resembling the tactile and Pacinian corpuscles, though smaller than either. The dermis with its papillæ is richly supplied with bloodvessels and lymphatics, as well as nerves. The arteries penetrating the dermis from beneath end in a capillary network, the latter extending as single loops into the papillæ, while the veins, more numerous and larger than the arteries, terminate in the superficial venous trunks. The lymphatics already referred to are most numerous on the fore and inner part of the body and limbs, being particularly well developed in the palms and soles. The dermis consisting largely of white fibrous tissue is by boiling resolved, in a great measure, into gelatine, the ordinary source of glue, hence, also its conversion into leather by tanning. The fibrous structure of the dermis, the papillæ, the mouths of hair follicles, etc., may usually be seen in the cut edge and rough surface of a piece of leather. Deprived of its fatty matters, etc., the dermis, when properly thinned, forms also parchment.

The epidermis, also known as the cuticle or scarf skin, constituting the superficial layer of the skin, bears the same relation to the dermis that the epithelium does to the deeper layer of mucous membranes.



Indeed, the transition of skin into mucous membrane at the mouth and anus is so gradual, that it is impossible to say where one ends and the other begins; in fact, as well known, if the skin be inverted in these places, it becomes mucous membrane, and if the mucous membrane be everted, it becomes skin. The internal surface of the epidermis is applied directly to the papillæ (Fig. 430) of the dermis,

FIG. 430.



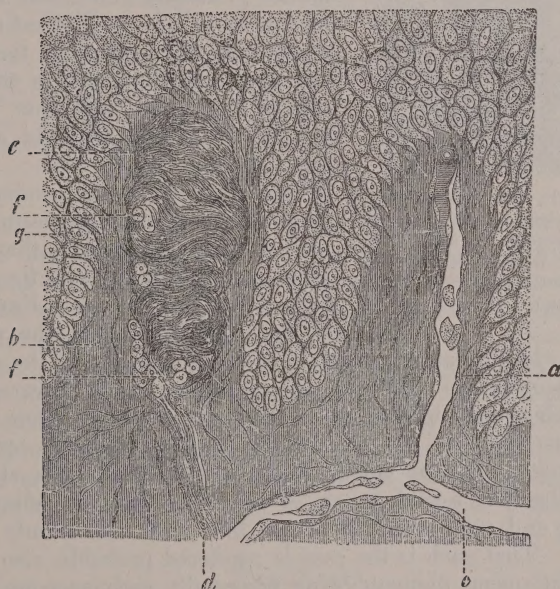
Epidermis elevated so as to show papillæ. (HIRSCHFELD.)

and follows closely all their inequalities; its external surface is marked by very shallow grooves corresponding to the furrows between the latter. The epidermis is entirely destitute of bloodvessels and lymphatics, deriving its nutritive fluid (like all other vascular parts), by osmosis, from the blood of the dermis. It was for a long time supposed that the epidermis was also without nerves. Recent investigations, however, make it probable that some of the cutaneous nerves pass through the dermis, terminating as non-medullated nerve fibres among the deeper layers of the epidermis in slightly bulbous-like extremities, or in a plexus of fine fibrils. However this may be, impressions made upon the epidermis will be appreciated, whether the latter be provided with nerves or not, being transmitted through pressure to the exquisitely sensitive dermis beneath. The epidermis serves as a protective covering to the soft and delicate dermis, which would be otherwise constantly exposed to laceration and drying.

Indeed, if the epidermis be removed, contact of the atmosphere alone will inflame the dermis, which, after death, rapidly dries. The epidermis is therefore thicker in those parts which are most exposed, as in the palms and soles, where it may measure as much as the  $\frac{1}{12}$ th of an inch or more, being very thin, on the other hand, upon the face, the eyelids, and in the external auditory meatus, attaining in these situations only a size of the  $\frac{1}{600}$ th to the  $\frac{1}{900}$ th of an inch. The whole skin then, including the dermis, in its thickest part would measure about the  $\frac{1}{5}$ th of an inch, and in its thinnest part about the  $\frac{1}{66}$ th of an inch. The thickness of the epidermis is, however, dependent to a great

extent upon the amount of pressure to which the skin is subjected, being very thick in the palm of the laborer and the sole of the plowman. Corns are thickened portions of the epidermis, and are due to the parts affected being exposed to excessive pressure or friction, hence they are developed not only in the feet by tight shoes, but on the knee of the shoemaker by constant hammering, and in front of the clavicle of the soldier by the pressure of the musket. The pain caused by corns is due to inflammation of the dermis, which they excite by pressing upon its delicate structure, just as any foreign body, a small stone, will do under similar circumstances. The epidermis consists of two layers, the rete mucosum and the cuticle. The rete mucosum or Malpighii, with a thickness varying from the  $\frac{1}{1700}$ th to the  $\frac{1}{75}$ th of an inch, constituting the deeper internal soft layer of the epidermis, is moulded upon the adjoining surface of the dermis, and when separated by maceration or putrefaction presents impressions corresponding exactly with the papillæ, furrows, depressions, etc., of the latter, the more prominent irregularities of the dermis being, as already mentioned, visible upon the outer surface of the cuticle, but less distinctly (Fig. 431). The

FIG. 431.



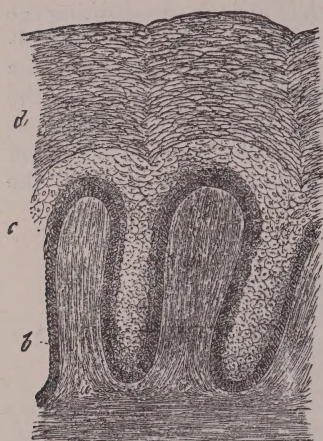
Rete mucosum.

rete mucosum consists of several irregular layers of cells of different forms, more or less agglutinated together. Those lying next to the dermis are somewhat elongated in figure, varying in length from the  $\frac{1}{4000}$ th to the  $\frac{1}{2000}$ th of an inch, and disposed perpendicularly, while the succeeding ones are of a rounded form and often marked with ridges and furrows, in sections appearing as spines. As the cells are gradually



pushed from below upward through the continual development of new cells at the surface of the dermis, they become more and more flattened, lose their soft granular contents and nucleus, and, becoming keratose, give rise to the different layers of the rete mucosum, and are finally transformed into the dry horny scales of the cuticle. While in the white race the cells of the rete mucosum are colorless and like those of the cuticle translucent, allowing the color of the underlying dermis to be seen, in those of the black races, the negro especially, the deeper ones (Fig. 432) are filled with brown or black pigmentary

FIG. 432



Skin of the negro, vertical section, magnified 250 diameters *a*, *a*. Cutaneous papillae. *b*. Undermost and dark-colored layer of oblong vertical epidermis-cells. *c*. Mucous or Malpighian layer. *d*. Horny layer. (KÖLLIKER.)

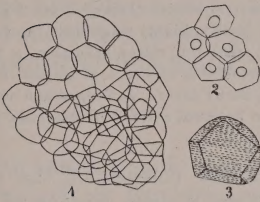
matter, which gives rise to their characteristic dark color, and, when present in smaller quantities, to the various shades of complexion of other races, of different individuals, and of different parts of the skin of the same individual, while the accumulation of this pigmentary matter in spots causes freckles. As the cells of the deeper layers of the rete mucosum are gradually transformed into those of the cuticle, the pigmentary matter gradually diminishes and finally disappears. It is interesting in this connection to note that the color of the dermis in the negro is the same as that of the white, and that the whole skin of the negro foetus is as pale as that of the white one. The fact of the pigment being developed in the deep cells of the rete mucosum only at or after birth would indicate that the black race had descended from the white one rather than the reverse. Further, since in the dark races and the semi-burnt

ones of the white races, the pigment is developed, not in the superficial, but in the deep layers of the rete mucosum, it is to be inferred that the pigment is eliminated by the cells of the rete mucosum from the blood of the dermis, and that the effect of the heat of the sun in temperate or tropical climates is not to modify directly the color of the skin, but in rendering the liver torpid, to throw upon the skin the elimination of the coloring and other matters of the bile, and, hence, only indirectly affecting it. That such is the case is rendered probable also from the fact of the cutaneous pigment being essentially carbonaceous in nature, as is that of bile. While there is no doubt that the cells of the rete mucosum are gradually transformed into those of the cuticle, there is considerable doubt as to whether they themselves are derived from those of the dermis, since, as we shall see hereafter, the epidermis is derived from the epiblast or external blastodermic membrane of the embryo, and the dermis from the mesoblast or middle blastodermic membrane. Such being the case, it is more probable that the deep epidermal cells

of the adult are derived by unbroken descent from the original epiblastic ones of the embryo than from those of its dermal mesoblastic ones.

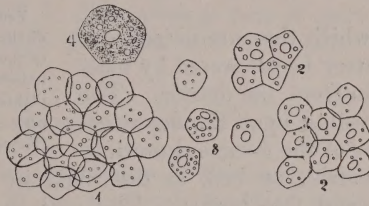
The cuticle, or cuticula, constituting the most external superficial portion of the epidermis, consists of numerous layers of hard, flattened, nearly dry, yellowish translucent cells, irregularly polygonal in form, generally granular, but without nuclei, measuring from the  $\frac{1}{2000}$ th to  $\frac{1}{750}$ th of an inch in diameter, and composed chemically of keratin, or horny matter; the deeper cells being rather thicker and rounder than those of the superficial layers. As the deeper surface of the cuticle is being continually renewed by fresh cells from the rete mucosum, its free surface is as constantly worn away, or shed off in flakes, constituting the so-called scurf (Fig. 433) and dandruff (Fig. 434). In

FIG. 433.



Scurf from the leg 1. A fragment of scurf, consisting of dried, flattened, non-nucleated cells or scales. 2. A few cells with a nucleus. 3. A cell more highly magnified, to exhibit its polyhedral form. (LEIDY.)

FIG. 434.



Fragment of dandruff from the head. 1. Portion of dandruff, consisting of non-nucleated cells. 2. Several fragments, consisting of nucleated cells. 3. Isolated cells, some with and without nuclei. 4. A cell more highly magnified, exhibiting granular contents and a nucleus. (LEIDY.)

many of the lower animals, as in snakes, for example, the cuticle exfoliates from time to time entire. By treating the cuticle with a solution of potash its scales separate from one another, swelling up into vesicles; it is for this reason that alkaline solutions remove the epidermis. In tanning, for example, the epidermis is removed by macerating the skin in lime, etc. A blister or burn, in producing inflammation of the dermis and effusion of liquid, breaks up the soft cells of the rete mucosum, and so elevates the cuticle. If the skin be macerated after death, the cuticle, through disorganization of the rete mucosum, detaches itself, and when under such circumstances, it is thick and strong, as in the case of the hand and foot, it may be stripped off like a glove.

## THE NAILS.

The nails, or ungues, appendages of the skin, corresponding to the claws and hoofs of other animals, and situated upon the dorsal surfaces of the distal phalanges of the fingers and toes, not only serve to protect these parts, but are also important as prehensile organs, in civilized races more especially, in the case of the fingers, but in certain barbarous ones, in that of the toes as well. The nails are thin, flexible, translucent quadrilateral plates, continuous with the epidermis (Fig. 435),



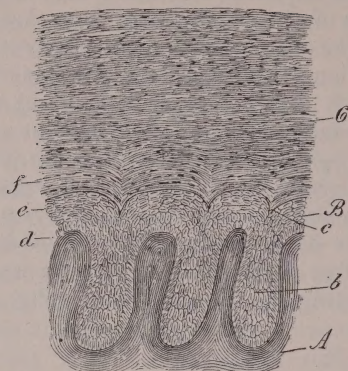
FIG. 435.



Vertical section of the end of a finger. 1. Epidermis on the back of the finger. 2. Point at which it is reflected to become continuous with the nail. 3. The nail. 4. Epidermis at the end of the finger. 5, 6, 7, 8 Surface of the dermis corresponding with the position of the soft epidermic layer. 9, 10, 11, 12. Dermis. 13. Last phalanx. 14. Flexor tendon. (LEIDY.)

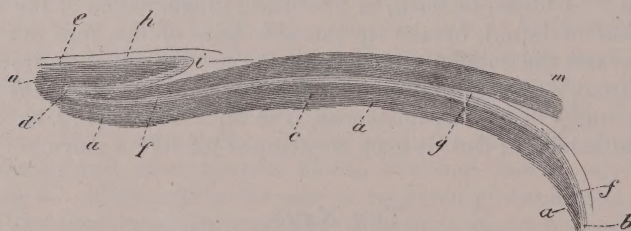
with which they are detached if the latter be separated by maceration from the dermis. The nail resting upon the depressed surface of the dermis, known as the matrix, or bed, as described by anatomists, consists of the root, body, and free border. The root is lodged in a deep groove of the matrix, the vallecule unguis, while the lateral borders of the body of the nail fit into rather shallow grooves, the free border of the nail being that part detached from the skin. The color of the nail is due to its translucency, which allows the color of the highly vascular, or underlying dermis, or matrix, to be seen; the lunula, or whitish spot at the root, defined by the semicircular line, is due to the matrix being there less vascular. The grooves exhibited more particularly on the under surface of the nail are the impressions made by the fine longitudinal ridges and papillæ of the dermis of matrix upon

FIG. 436.



Vertical transverse section through a small portion of the nail and matrix, highly magnified. A. Corium of the nail-bed, raised into ridges, or laminae, *a*, fitting in between corresponding laminae, *b*, of the nail. B Malpighian, and C, horny layer. *d*. Deepest and vertical cells. *e*. Upper flattened cells of Malpighian layer. (KÖLLIKER.)

FIG. 437.



Longitudinal section through the middle of the nail and bed of the nail. *a*. Bed of the nail, and cutis of the back and points of the fingers. *b*. Mucous layer of the points of the fingers. *c*. Of the nail. *d*. Of the bottom of the fold of the nail. *e*. Of the back of the finger. *f*. Horny layer of the points of the fingers. *g*. Beginning of them under the edge of the nail. *h*. Horny layer of the back of the fingers. *i*. Ends of it upon the upper surface of the root of the nail. *k*. Body. *l*. Root. *m*. Free edge of the proper substance of the nail. Magnified 8 diameters.

which the nail is moulded. The nail, like the epidermis, consists of two layers—a horny layer, and a soft layer. The soft layer corre-

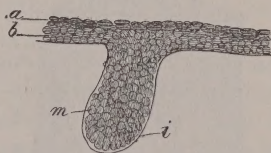
sponding to the rete mucosum of the epidermis, consists, like the latter, of delicate, polyhedral nucleated cells, averaging from the  $\frac{1}{3000}$ th to the  $\frac{1}{1700}$ th of an inch in length, which are being continually transformed into the scales of the horny layer. The latter, corresponding to the cuticle of the epidermis, consists of a number of layers of flattened nucleated cells, or scales, varying from the  $\frac{1}{1000}$ th to the  $\frac{1}{750}$ th of an inch in diameter, but so intimately associated that they can only be recognized under the microscope, after separation from one another by treatment with alkalis, etc. The thickness of the true nail—that is, of its horny layer at the root—is from the  $\frac{1}{200}$ th to the  $\frac{1}{100}$ th of an inch, and at the middle of the body of the nail, from the  $\frac{1}{40}$ th to the  $\frac{1}{30}$ th of an inch. Through the constant addition of cells, the root of the nails grows in length, and through addition of the cells beneath, in thickness—the free cut edge of the nail consisting of the horny layer only. (Fig. 437.) The average rate of growth of the nails is said to be  $\frac{1}{32}$ d of an inch per week, and to be more rapid in summer than in winter.<sup>1</sup>

## THE HAIRS.

The hairs, or pili, like the nails, appendages of the skin, and more particularly of the rete mucosum of the epidermis, are first noticed at about the third or fourth month of intra-uterine life, as little black specks beneath the cuticle, consisting of a mass of cells, defined by a basement membrane (Fig. 438), developed through invagination, or the growing downward of the cells of the rete mucosum into the dermis. As development advances, the cells of which this flask-like body consists are differentiated into a central and a lateral portion (Fig. 439, A), the former the rudiment of the future hair, the latter the root-sheath, or the lining of the hair follicle, while the projecting of the dermis into the bottom of the flask-like hair forms its papillæ. With the gradual upward growth of the hair and the development of the different parts, of which, as we shall see, it consists (Fig. 439, B, C), the root-sheath divided into the inner and outer root-sheaths, the former, except at the bottom, subdividing into Huxley's and Henle's layers, the latter being surrounded and defined by a fibrous membrane, derived from the dermis, and constituting the wall of the hair follicle.

Finally, the hair, being fully formed, penetrates the cuticle, the papilla to which it is attached having been provided with nervous filaments and capillary bloodvessels. The hair is usually described as consisting of a root beginning in the skin as a club-like expansion,

FIG. 438.

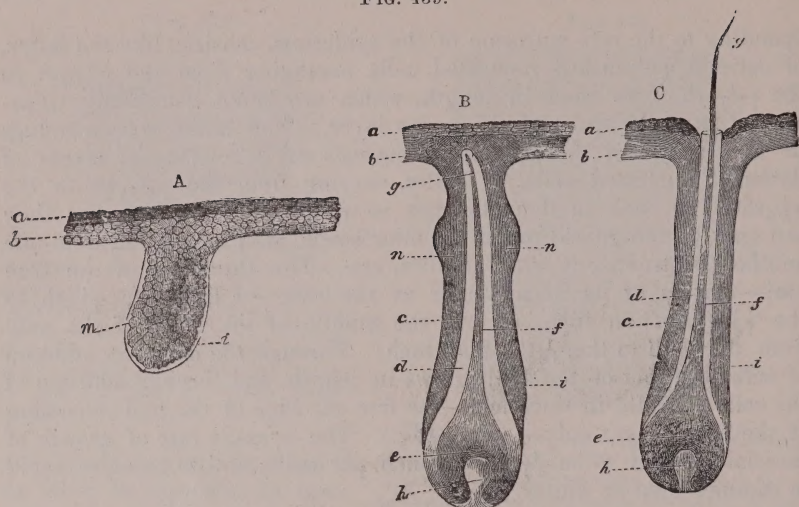


Rudiment of the hair from the brow of a human embryo, sixteen weeks old; magnified 350 diameters. *a*. Horny layer of the epidermis. *b*. Its mucous layer. *i*. Structureless membrane surrounding the rudiment of the hair, and continued between the mucous layer and the corium. *m*. Roundish, partly elongated cells which especially compose the rudiments of the hair.

<sup>1</sup> Quain's Anatomy, 1878, vol. ii. p. 219.



FIG. 439.



A. Hair rudiment from an embryo of six weeks. *a*, Horny, and *b*, mucous or Malpighian layer of cuticle. *i*, Basement membrane. *m*, Cells, some of which are assuming an oblong figure, which chiefly form the future hair. B. Hair rudiment, with the young hair formed, but not yet risen through the cuticle. *a*, Horny. *b*, Malpighian layer of epidermis. *c*, Outer, *d*, inner root sheath. *e*, Hair-knob. *f*, Stem, and *g*, point of the hair. *h*, Hair-papilla. *n, n*, Commencing sebaceous follicles. C. Hair-follicle with the hair just protruded. (SCHÄFER.)

FIG. 440.

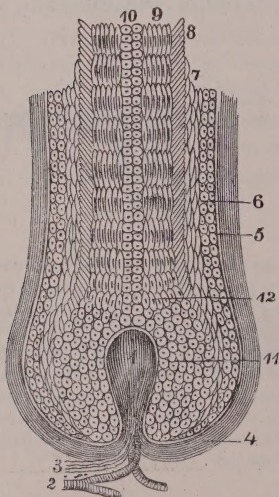


Diagram of structure of the root of a hair within its follicle. 1. Hair papilla. 2. Capillary vessel. 3. Nerve fibres. 4. Fibrous wall of the hair follicles. 5. Basement membrane. 6. Soft epidermis, lining of the follicle. 7. Its elastic cuticular layer. 8. Cuticle of the hair. 9. Cortical substance. 10. Medullary substance. 11. Bulb of the hair composed of soft polyhedral cells. 12. Transition of the latter into the cortical substance, medullary substance, and cuticle of the hair. (LEIDY.)

the bulb and a shaft or stem projecting from the skin, and terminating in the end or point. It is composed (Fig. 440) usually of a medulla, or central axis, around which are concentrically disposed the cortical substance and cuticle. The medulla consists of cuboidal cells, having a diameter of from the  $\frac{1}{2000}$ th to the  $\frac{1}{1200}$ th of an inch, with granular contents, and an indistinct nucleus, usually intermingled with small bubbles of air, which have penetrated from the ends of the hair, and, when present, giving rise to the white silvery lustre of the latter. In downy hairs the medulla is absent. The cortical substance, or the cortex, constitutes the chief bulk of the hair, and is that part upon which the color of the hair principally depends in different individuals and races. It is composed of several layers of flexible fibres, the latter consisting of elongated fusiform cells. With the loss of the coloring matter, which is generally diffused through the cortical substance, the latter becomes white. The cuticle consists of a single layer of thin colorless quadrilateral cells, overlapping each other like the shingles of a roof. The edges of these scales

being directed upward and outward along the shaft offer an obstacle to any movement of the hair otherwise than with its root forward when rubbed between two surfaces. It is upon this fact that the felting of hair and wool of various animals depends. The hair, like the epidermis, being destitute of bloodvessels, derives its nutritive liquid by osmosis from the blood of the vessels of the papilla. While analogy would lead one to suppose the nerve filaments of the papilla penetrate the hair, as a matter of fact, no nervous filaments having as yet been demonstrated in it, any sensibility that the hair may possess must depend, therefore, upon that of the papilla which the hair bulb tightly encloses or caps. The hairs are continually renewed by constant growth. In some instances, especially after disease, they are cast off or shed, new ones being produced. Permanent baldness is due to atrophy of the papillæ, while the sudden blanching of the hair, occurring sometimes in a single night, is due to the greater part of the medulla and cortex becoming filled with air.<sup>1</sup>

Chemically, hairs are composed of fats, a gelatine-like substance, albuminous matters, containing a large proportion of sulphur, peroxide of iron, traces of manganese, silica, sodium, and potassium chlorides, calcium sulphate and phosphate, and magnesium sulphate.<sup>2</sup> With the exception of the palms of the hands and soles of the feet, the palmar surface of the fingers and toes, the lips, lining of the prepuce and glans penis, hairs cover nearly every part of the surface of the body. The hairs generally project obliquely from the skin, and are regularly disposed, usually in curving lines from particular points. They differ very much as regards their size, fineness, color, form, and number, in different races, sexes, individuals, and parts of the body. Of the long hairs, attaining sometimes in women a length of three feet or more, and a diameter of from the  $\frac{1}{500}$ th to the  $\frac{1}{400}$ th of an inch, the finest are found upon the head. The short, stiff hairs of the nostrils and edges of the eyelids, are from the  $\frac{1}{400}$ th to the  $\frac{1}{170}$ th of an inch in diameter, the fine downy ones from the  $\frac{1}{2000}$ th to the  $\frac{1}{1200}$ th. While the fine silken hair of the head in the white race is cylindrical, the crisp hair of the head and beard of the negro is more or less flattened cylindrical. It has been estimated<sup>3</sup> that upon a square inch of scalp there are about 1000 hairs, the number upon the entire head amounting to 120,000. The hairs are elastic, readily electrified by friction, especially in cold, dry weather, and very hygrometric. The latter property is taken advantage of in the making of delicate hygrometers, the hair elongating through the absorption of moisture. The hairs not only serve to protect the general surface, as in shielding the head from excessive cold or heat, but also guard certain orifices, as those of the ears and nose. The eyebrows prevent the perspiration from the forehead running on to the lids, the eyelashes the surface of the conjunctiva from dust, etc. Hair, being a bad conductor of heat, serves also to retain that produced within the body. It has already been mentioned that the hairs are quite regularly disposed, and it will be further observed that

<sup>1</sup> Landois: Virchow's Arch., 1866, Band xxv. S. 375. Wilson: Proc. Roy. Soc. Lond., 1867, vol. xv. p. 406.

<sup>2</sup> Quain's Anatomy, vol. ii. p. 226.

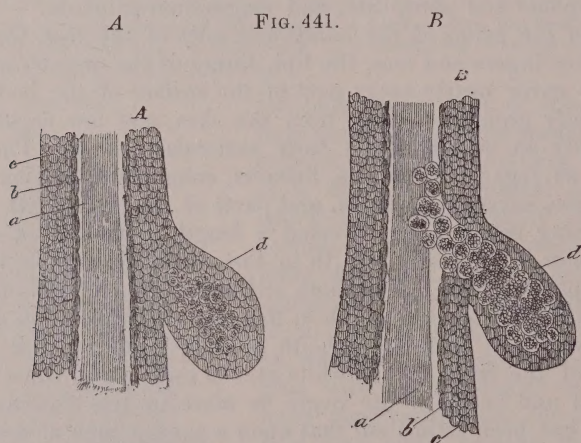
<sup>3</sup> Wilson: Healthy Skin, p. 84. Philadelphia, 1854.



if a man assume a crouching attitude, with elbows upon the knees, and the chin resting upon the hands, that their general direction upon the extremities is obliquely downward, a disposition such, that if the person be exposed to wet weather, the rain will be drained off, an effect obviously of advantage to the primitive man, as well as to those who go naked at the present day. Finally, the hairs may be regarded, to a certain extent at least, as so many excretory organs, since their growth necessarily involves the excreting from the blood the different principles of which we have seen that they chemically consist, and which, if retained within the system, in all probability would give rise to disease.

### SEBACEOUS GLANDS.

The sebaceous glands, like the nails and hair, are appendages of the epidermis, being developed during the fourth and fifth months of intra-uterine life as outgrowths of the hair follicles, into which, with but few exceptions, they eventually open. Each sebaceous gland begins (Fig. 441, *A*) as a solid bud sprouting out into the dermis from the external



The development of the sebaceous glands in a six months' fetus. *a*. Hair. *b*. Inner root-sheath, here more closely resembling the horny layer of the epidermis. *c*. Outer root-sheath. *d*. Rudiments of the sebaceous glands. *A*. Flask-shaped rudiments of the gland, with fat developed in the central cells. *B*. Larger rudiments. (KÖLLIKER.)

root sheath of the hair follicle, and consists entirely of nucleated cells. As development advances, however, the cells in the central portion of the flask-like (Fig. 441, *B*) bud develop fat, which, gradually extending themselves, penetrate the root-sheaths of the hair follicle, and so pass into the cavity of the latter as the primitive sebaceous secretion, while through the further division and subdivision of the primitive bud the latter assumes the form of a simple or compound racemose gland. The sebaceous gland when fully developed consists of a delicate wall of fibrous tissue defined by a basement membrane lined with an epithelium consisting of polyhedral nucleated cells, with granular

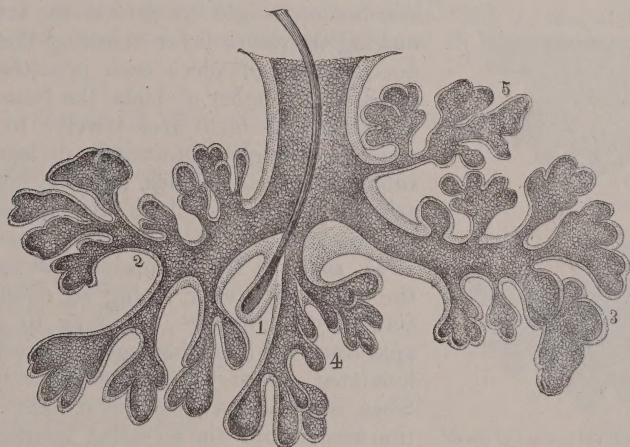
contents, the cavity of the gland being filled with sebaceous matter, the chemical composition of which is given in Table LXXV., and

TABLE LXXV.<sup>1</sup>—COMPOSITION OF SEBACEOUS MATTER.

|                                            |     |
|--------------------------------------------|-----|
| Water . . . . .                            | 357 |
| Olein . . . . .                            | 270 |
| Margarin . . . . .                         | 135 |
| Sodium butyrate and butyric acid . . . . . | 3   |
| Casein . . . . .                           | 129 |
| Albumen . . . . .                          | 2   |
| Gelatin . . . . .                          | 87  |
| Sodium } phosphate . . . . .               | 7   |
| Calcium                                    |     |
| Sodium chloride . . . . .                  | 5   |
| Sodium sulphate . . . . .                  | 5   |
| <hr/>                                      |     |
| 1000                                       |     |

consisting physically of cells and oil globules, the cells containing granular matter and more or less distended with oil. The sebaceous glands are very numerous, existing almost everywhere, except in the palms and soles. Usually associated with the hair follicles (Fig. 442),

FIG. 442



A large gland from the nose, with a little hair-sac opening into it; magnified fifty diameters.  
(KÖLLIKER.)

they are disposed around the latter in groups varying from two to eight to each follicle, and imbedded in the more superficial part of the dermis, appearing as round whitish bodies, and measuring on an average from the  $\frac{1}{120}$ th to the  $\frac{1}{50}$ th of an inch in diameter. The largest sebaceous glands are those of the nose, concha of the ear, skin of the penis, the scrotum, labia, and areola surrounding the female nipple.

The use of the sebaceous matter is to smear the hairs with oil as they grow out of the skin and thoroughly to imbue the cuticle with the same, through which it is rendered repellant of water. The

<sup>1</sup> Robin : Leçons sur les humeurs, p. 599. Paris, 1867.

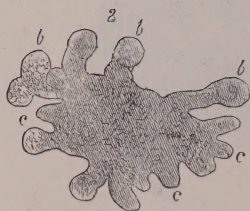
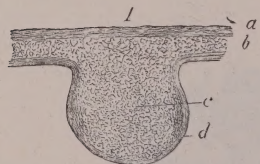


greasiness of the skin thus produced is the cause of smut and dirt adhering to the person so readily and necessitating the use of soap for the removal of the same. The too free use of alkaline washes, however, in depriving the cuticle of its natural oil renders the skin dry and harsh. The sebaceous matter often becoming inspissated, distends the glands producing it, especially in those of the nose, and becoming incorporated at the mouth of the duct with dirt if squeezed out is often regarded on account of the shape as a worm, the dirt being supposed to be the head. It should be mentioned, however, that the sebaceous matter frequently contains the so-called pimple mite, the *acarus* or *Demodex folliculorum*. The sebaceous glands somewhat modified constitute also the Meibomian glands of the eye, the description of which will be deferred, however, till the organ of vision is considered.

### MAMMARY GLANDS AND MILK.

The mammary, like the sebaceous glands just described, are also appendages of the epidermis, being developed in the fourth or fifth

FIG. 443.



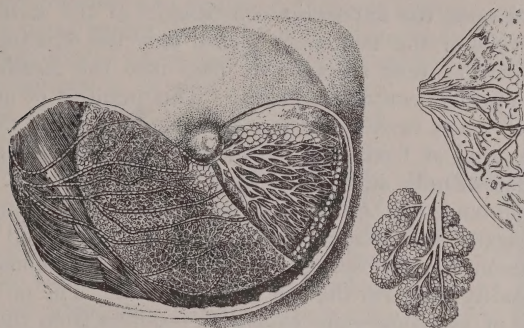
Development of the lacteal gland. 1, rudiment of the gland in a male embryo, at five months; *a*, horny layer; *b*, mucous layer of the epidermis; *c*, process of the latter or rudiment of the gland; *d*, fibrous membrane around the same. 2, lacteal gland of a female fetus, at seven months, seen from above; *a*, central substance of the gland, with larger (*b*) and smaller (*c*) solid outgrowths, the rudiments of the large gland lobes.

month of intrauterine life (Fig. 443, 1, 2) as solid invaginations or projections of the rete mucosum into the dermis, the latter furnishing the dense layer investing them. As development advances each primitive gland gives off a number of buds, the future lobes, numbering at birth from twelve to fifteen, which, through continued division and subdivision into lobules, and the latter into acini or secreting vesicles, ultimately assume the constitution of a racemose gland (Fig. 444), such as the parotid or submaxillary, the whole, however, being so closely associated by connective tissue as to give the appearance of being homogeneous rather than lobulated. Just before the ducts from the lobes reach the nipple they expand beneath the areola into the so-called lactiferous sinuses, especially observable in the human female during lactation, and constituting the large milk reservoirs in the cow. As the lacteal or galactophorous ducts from each lobe terminate at the summit of the nipple in a small orifice, the number of the latter, usually twelve to fifteen, correspond with the number of lobes. The mamma, as a whole, is of a firm consistence: of a pinkish-white color, of circular form with its external

surface convex and prolonged to the nipple. The latter, provided with sensitive papillæ, is highly vascular and capable of erection. The nipple, reddish or brownish, is surrounded by an areola of skin usually

of the same color, and containing sebaceous glands appearing as whitish eminences, which, during sucking, secrete a fatty substance which

FIG. 444.



protects the part from excoriation. The mammæ exist in the male, but usually only in a rudimentary condition. Their presence in animals gives rise to the name mammalia, the highest order of vertebrates, and while as a general rule, they are attached in such to the abdominal walls, in man and monkeys they are situated on the anterior part of the thorax.

TABLE LXXVI.<sup>1</sup>—COMPOSITION OF HUMAN MILK.

|                     |           |         |
|---------------------|-----------|---------|
| Water               | . . . . . | 902.717 |
| Casein (desiccated) | . . . . . | 29.000  |
| Lacto-protein       | . . . . . | 1.000   |
| Albumen             | . . . . . | .....   |
| Butter              | . . . . . | 25.000  |
| Sugar of milk       | . . . . . | 37.000  |
| Sodium lactate      | . . . . . | 0.420   |
| Sodium chloride     | . . . . . | 0.240   |
| Potassium chloride  | . . . . . | 1.440   |
| Sodium carbonate    | . . . . . | 0.053   |
| Calcium carbonate   | . . . . . | 0.069   |
| Calcium phosphate   | . . . . . | 2.310   |
| Magnesium phosphate | . . . . . | 0.420   |
| Sodium phosphate    | . . . . . | 0.225   |
| Ferric phosphate    | . . . . . | 0.032   |
| Sodium sulphate     | . . . . . | 0.074   |
| Potassium sulphate  | . . . . . | .....   |
|                     |           | 100.000 |

|                   |   |               |           |       |                                |
|-------------------|---|---------------|-----------|-------|--------------------------------|
| Gases in solution | { | Oxygen        | . . . . . | 1.29  | } 30 parts per 1000 in volume. |
|                   |   | Nitrogen      | . . . . . | 12.17 |                                |
|                   |   | Carbonic acid | . . . . . | 16.54 |                                |

The secretion of the mammary glands or milk constituting a sort of emulsion, whose average composition is given in Table LXXVI., consists of a colorless liquid, the milk plasma, composed of water, holding in solution casein, milk, sugar, salts, etc., and innumerable fat-like

<sup>1</sup> Robin, op. cit., 1867, p. 95. Somewhat modified and authenticated. Error corrected.



bodies, the milk corpuscles, or globules. The latter, to which the opaque, whitish color of milk is due are very variable in size ( $\frac{1}{12000}$ th to the  $\frac{1}{1250}$ th of an inch), and consist of minute drops of fat surrounded apparently by a thin film of coagulated casein. With the exception of the water, and salts, the important constituents of the milk are elaborated by the cells of the mammary gland, they not existing as such in the blood, which, as they successively pass into the lactiferous ducts, burst, giving up their contents as milk. The quantity of milk secreted in twenty-four hours varies very much, depending upon the condition of the female, kind of food, etc. Perhaps it may be assumed that the daily production of milk amounts to from two to six pints. When milk coagulates spontaneously, or through the action of lactic acid upon the casein, it separates into the curd, composed of casein and most of the fat, and a greenish-yellow serum—the whey—the phenomenon taking place more readily in warm than in cold weather. The milk formed at the beginning of lactation—the colostrum—differs from the latter milk in being thinner, yellowish in color, and containing many of the milk cells in an entire condition; the colostrum corpuscles are somewhat in chemical composition, as given in Table LXXVII.

TABLE LXXVII.<sup>1</sup>—COMPOSITION OF COLOSTRUM.

|                            |                          |  |  |  |  |  |  |  |  |        |
|----------------------------|--------------------------|--|--|--|--|--|--|--|--|--------|
| Water . . . . .            |                          |  |  |  |  |  |  |  |  | 945.24 |
| Albumen . . . . .          |                          |  |  |  |  |  |  |  |  | 29.81  |
| Butter . . . . .           |                          |  |  |  |  |  |  |  |  | 7.07   |
| Sugar of milk . . . . .    |                          |  |  |  |  |  |  |  |  | 17.27  |
| Sodium                     | } chloride . . . . .     |  |  |  |  |  |  |  |  |        |
| Potassium                  |                          |  |  |  |  |  |  |  |  |        |
| Potassium                  |                          |  |  |  |  |  |  |  |  |        |
| Calcium                    | } phosphate and sulphate |  |  |  |  |  |  |  |  | 4.41   |
| Magnesium                  |                          |  |  |  |  |  |  |  |  |        |
| Ferric phosphate . . . . . |                          |  |  |  |  |  |  |  |  |        |

During the intervals of lactation the mammary glands secrete only a small quantity of viscid mucus.

#### SUDORIFEROUS GLANDS.

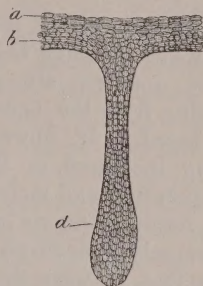
The sudoriferous or sweat glands, like the sebaceous and mammary glands, are appendages of the epidermis, beginning about the fifth month of intrauterine life as flask-like involutions of the cells of the rete mucosum of the epidermis into the dermis (Fig. 445). As development advances this solid flask-like rudiment becomes transformed into a hollow tube, which, extending itself through the dermis to the subcutaneous adipose tissue, terminates at the one end in a coil, and at the other end as the sweat pore on the surface of the skin, a passage-way in the meantime being formed in the epidermis leading from the latter into the hollow tube. Each sweat gland, when fully formed, consists of a tube convoluted at its commencement, the secreting portion of a yellowish-red color, spheroidal in form, with an average diameter of the one-twentieth of an inch, and passing thence upward, as the sweat

<sup>1</sup> Robin, op. cit., p. 409.

duct, in a slightly tortuous manner to the external surface of the dermis. The tube consists of an external fibrous layer, succeeded by a basement membrane, the latter supporting an epithelium of polyhedral nucleated cells containing granular and yellowish pigment matter. As just mentioned, at the point where the sweat duct opens on the surface of the dermis a passage-way is continued through the epidermis to the exterior. Where the epidermis is thin the passage way is straight, but where thick, as in the palms and soles, it takes a spiral course, terminating at the surface in a funnel-shaped orifice. The openings of the sweat ducts may be distinctly seen disposed in a single row of the summits of the ridges of the skin of the palms and soles, if the latter be viewed with a common pocket lens. In other situations, however, they are far less apparent. With the exception of the concave surface of the concha of the ear, the glans penis, the inner layer of the prepuce, and perhaps a few other places, the sweat glands are found in every part of the skin. The number varies, however, very much according to the part of the skin examined. Thus, while according to Krause,<sup>1</sup> in the palmar surface of the hand there may be as many as 2736 sweat glands to the square inch of skin, in that of the nates there may be as few as 417 per square inch. It is this variation in the number of sweat glands existing in different parts of the skin that renders any determination as to their total number, as estimated, for example, by Krause at 2,381,248, so very uncertain. Assuming that the secreting portion of the coil of each sweat duct, when unravelled, measures the one-sixteenth of an inch in length on the above estimate, if the tubes were placed end to end they would extend a distance of two and one-third miles. It should be mentioned, however, with reference to this last estimate, that the length of the excretory portion of the duct is not taken into consideration, which will depend on the thickness of the skin. Supposing the latter to be one-fifth of an inch, the mean of its thickest and thinnest parts, the total length of the excretory portion of the sweat ducts would amount to seven and one-half miles, a somewhat exaggerated estimate, and very approximate, it must be admitted. The sweat glands, somewhat modified, constitute the ceruminous glands of the ear, which will be referred to again in our account of that organ, and also the odoriferous glands of the axilla.

In the latter situation they form a patch in the subcutaneous connective and adipose tissue often an inch and a half or more in diameter, being largest in the centre of the patch and gradually diminishing toward the circumference, where they become undistinguishable from the ordinary sweat glands. The odoriferous glands of the axilla not

FIG. 445.



Rudiment of a sudoriparous gland of a human embryo at five months. Magnified 350 diameters. *a.* Horny layer of the epidermis. *b.* Mucous layer. *c.* Corium. *d.* Rudimentary glands, as yet without any cavity, and consisting of small round cells.

<sup>1</sup> Wagner's Physiology, Band ii. S. 131. Braunschweig, 1844.



only secrete sweat but a strongly odorous substance, hence their name, which varies somewhat in character in the different races of mankind. Indeed, it is to this secretion that the peculiar odor of negroes is to a great extent to be attributed, the glands as a general rule being better developed in the negro than in the white man as shown first by the late Professor Horner,<sup>1</sup> attaining in the negro the size of a pea.

#### PERSPIRATION.

The secretion of the sudoriferous or sweat glands, the perspiration or sweat, although being continually elaborated by the latter from the blood, does not always appear as such upon the surface of the skin, passing from the body in the form of an insensible vapor as rapidly as produced. If, however, through the amount of the sweat secreted being increased, or from the condition of the atmosphere, as regards temperature and moisture, the whole of the sweat produced evaporates, the residue remains in the form of minute drops, and constitutes what is commonly understood as sweat or perspiration. There is no difference, therefore, between the insensible and sensible perspiration, the form in which it may be exhaled, whether as liquid or vapor, depending simply upon the conditions just mentioned.

Sweat is a clear watery liquid, of a specific gravity of 1.003 to 1.004, having a saline taste and a peculiar odor according to the part of the skin from which it is obtained. The reaction of the sweat appears to be alkaline, the acidity often observed being due probably to decomposition and to the presence of certain volatile acids, such as the acetic, formic, butyric.

Sweat, as shown in Table LXXVIII., is composed in by far the greater part of water, urea, fatty matters, salts, epidermic scales in small quantities, together with from the  $\frac{1}{50}$ th to the  $\frac{1}{200}$ th of the carbonic acid produced in the system, using the word sweat in its fullest acceptance.

TABLE LXXVIII.<sup>2</sup>—COMPOSITION OF SWEAT.

|                               |                 |
|-------------------------------|-----------------|
| Water . . . . .               | 995.573         |
| Urea . . . . .                | 0.043           |
| Fatty matters . . . . .       | 0.014           |
| Alkaline lactates . . . . .   | 0.317           |
| “ sudorates . . . . .         | 1.562           |
| Sodium chloride . . . . .     | 2.230           |
| Potassium chloride . . . . .  | 0.244           |
| Alkaline sulphates . . . . .  | 0.012           |
| “ phosphates . . . . .        | .....           |
| “ albuminates . . . . .       | 0.005           |
| “ earthy phosphates . . . . . | .....           |
| Debris (epidermis) . . . . .  | 0.000.000       |
|                               | <hr/> 10000.000 |

So far as known to the author, the celebrated Sanctorius was the first to endeavor to determine experimentally, during the seventeenth century, the amount of the perspiration, the method made use of being to

<sup>1</sup> American Journal of Med. Sciences, 1846, p. 13.

<sup>2</sup> Faivre: *Archiv Générales de Médecine*, 5 ième serie, tome ii. p. 1. Paris, 1853.

weigh daily the body and all the solid and liquid ingesta and egesta, and from the loss of weight experienced by the body to deduce the amount of vapors transpired. Thus, if from every 8 pounds of ingesta taken in 24 hours there were 3 pounds of sensible egesta, 44 ounces of urine, and 4 ounces of feces, it was inferred that the remaining 5 pounds of ingesta passed from the body insensibly in the form of vapor. Unfortunately, however, as the latter included the vapor exhaled from the lungs as well as that from the skin, and the observation simply embodied as aphorisms,<sup>1</sup> no numerical tables given, the results obtained have now but little value, although Sanctorius experimented daily in the manner described for a period of thirty years. Although numerous and interesting observations and experiments were made during the eighteenth century by Dodart, Keill, Rye, Gorter, Lining, Hales, Stark, with a view of determining the amount of the perspiration and the conditions affecting it; it will not be necessary to dwell upon them, since the pulmonary and cutaneous perspiration were estimated together by these observers. The first attempt to estimate separately the vapor exhaled by the skin from that by the lungs was made by Lavoisier<sup>2</sup> and Seguin in 1790, the experiments consisting in enclosing Seguin in a bag of gummed taffeta which was tied above the head, an aperture in the coat when fixed around the mouth by a mixture of turpentine and pitch enabling Seguin to inspire fresh air and exhale the breathed air, but only permitting the pulmonary vapor of the latter to escape from the body. By then deducting the amount of the pulmonary vapor as determined by the loss of weight when enclosed in the gum coat from the total quantity of vapor exhaled as determined by the loss of weight when so enclosed, the amount of the cutaneous vapor was at last experimentally determined, and was found to be nearly two pounds, one pound and fourteen ounces, which does not differ very considerably from the later results obtained by Krause<sup>3</sup> and Valentin.<sup>4</sup>

The amounts of perspiration exhaled by the skin, as shown by Lavoisier and Seguin and subsequent observers, vary very considerably, however, depending upon the quantity and temperature of the liquid food, the relative dryness or moisture and temperature of the atmosphere, the amount of exercise taken, and the activity of the lungs and kidneys, with which the skin acts vicariously. The skin, however, not only supplements the action of the lungs as regards the exhalation of watery vapor and carbonic acid, but that of the kidneys also, and not only with reference to the water but to the urea eliminated as well. Thus, according to Carpenter,<sup>5</sup> in one experiment the entire quantity of perspiration for the whole body being in one hour 3320 grains,  $6\frac{1}{2}$  grains of urea, containing 3.03 N, were obtained. It is not likely, however, that the excretion of urea would have continued during the whole twenty-four hours at such a rate. It should be mentioned in this connection also, according to Funke,<sup>6</sup> that through the desquamation of the epidermic scales about eleven grains of nitrogen are also daily

<sup>1</sup> Sanctorii Sanctorii: De Statica Medecina aphorismorum. Lugduni Batavorum, MDCCIII.

<sup>2</sup> Mem. de l'Acad. des Sciences, p. 609. Paris, 1797.

<sup>3</sup> Physiologie, Band II. S. 319.

<sup>4</sup> Physiologie, Band I. S. 174. Braunschweig, 1844.

<sup>5</sup> Physiologie, p. 491.

<sup>6</sup> Moleschott Unters., 1858, Band iv. S. 56.



eliminated from the system by the skin. The fatty matters of the sweat are probably produced by the sebaceous glands, while, as regards the inorganic principles, the most notable is sodium chloride, existing in the proportion of 2.2 parts per thousand. That the sweat, however, contains other substances than those already mentioned is rendered very probable from the fact that death soon ensues when the perspiration is suppressed, as, for example, when the skin is varnished in animals<sup>1</sup> and also in human beings, as in the celebrated case of the child, who, being covered with gold-leaf to personate an angel at the coronation of Leo X., died a few hours afterward.<sup>2</sup> While death in such cases is no doubt partly due to the imperfect arterialization of the blood and the rapid fall of temperature, the varnish favoring the loss of heat in producing a cutaneous hyperæmia similar to that induced through paralysis of the vasomotor nerves, symptoms like that of uræmic poisoning, tremors, tetanic cramps, movements of rotation, increased reflex excitability, present as well, lead one to suppose that urea and other poisonous substances not yet isolated are retained in the system which are usually carried away in the sweat. That such is the case is shown by the fact that if human sweat be injected into the blood of the rabbit<sup>3</sup> the pulse of the latter may be increased from 192 beats per minute to 326, the respiration from 82 to 105, and the temperature raised from 99.2° to 104.3° F. Even if it be admitted that the exact cause of death is not yet positively determined there can be no doubt that imperfect action of the sweat-glands must be a source of disease, various matters then accumulating in the system which would otherwise be eliminated. Indeed, too much stress cannot be laid upon the importance of keeping the skin clean—of the free use of water. Especially is such the case in tropical climates where the true secret of maintaining one's health lies in attending to the condition of the skin, and where febrile diseases are more successfully treated by active diaphoresis than in any other way. The great importance of daily baths in the maintenance of health cannot be exaggerated, and apparently was more appreciated by the ancients than the moderns, as the ruins of the magnificent baths of Caracalla and Diocletian, at Rome, still to this day testify. Noble institutions they were; the baths or thermæ fed by stupendous aqueducts stretching for miles across the Campagna, their perpetual streams of hot and cold water flowing through mouths of solid silver into capacious basins, accommodating at one time thousands of bathers, and where for the eighth of an English penny the meanest Roman of them all could enjoy the luxury that might have well excited the envy of the kings of Asia.<sup>4</sup>

The secretion of sweat, like other secretions, is influenced by the nervous system, the sweat centre or centres being situated, according to Luchsinger,<sup>5</sup> in the anterior horns of the gray matter of the spinal cord and medulla. From these centres nerve fibres arise, which, passing down the cord, emerge principally with the anterior roots of the third, fourth, and fifth cervical nerves to pass with the brachial plexus

<sup>1</sup> Fourcaut : *Comptes Rendus*, tome vi. p. 369. Paris, 1838. *Ibid.*, 1843, tome xvi. p. 139. Valentin : *Archiv f. Physiologie Heilkunde*, 1858, Band ii. S. 433. Bernard : *Liquides de l'Organisme*, tome ii. p. 177. Paris, 1859.

<sup>2</sup> Laschkewitsch : *Du Bois-Reymond's Arch.*, 1868, S. 61.

<sup>3</sup> Rohrig : *Jahrb. f. Balneologie*, 1873, Band i. S. 1.

<sup>4</sup> Gibbon : *Decline and Fall of the Roman Empire*, vol. v. p. 237. London, 1807.

<sup>5</sup> Pfliiger's *Archiv*, Band xiii. S. 212; Band xiv. S. 545; Band xv. S. 482; Band xvi. S. 538.

to the skin of the upper extremity, and with the anterior roots of the lumbar nerves to supply the lower extremity. The sweat centres may be stimulated directly and reflexly. It is in the latter manner that the sweat centres are excited in man by motion, fear, heat, various substances such as pilocarpin, nicotin, muscarin, and inhibited by cold, and atropin.

The manner in which the skin regulates the temperature of the body through the radiation, conduction, etc., of the heat produced within it having already been sufficiently considered, it will not be necessary to treat further of the function of the skin in this respect. While there can be no doubt that absorption in the lower animals and in many of the higher, is to a considerable extent carried on by the skin, frogs, lizards, etc., rapidly gaining in weight when immersed in water, some difference of opinion still prevails among physiologists as to what extent the skin in man normally acts as an absorbing surface. It may not appear superfluous, therefore, if attention be called to those instances or conditions in which absorption does take place in man by the skin. It is well known, as already mentioned, in speaking of the cause of thirst, that in the case of the shipwrecked sailor the thirst was very much, if not entirely, temporarily relieved by the immersion of the body in the sea, or by wearing clothes wet with the same.<sup>1</sup> In certain cases also, where the introduction of solid or liquid food by the mouth had become impracticable, immersion of the patient in a bath of tepid milk morning and evening not only relieved the thirst, but for some time maintained life, the weight gained being unaccounted for by the enemata also given.<sup>2</sup> It has also been shown that not only does the body gain in weight after immersion in a bath through the absorption of the liquid, but that the skin will also absorb certain salts when dissolved in the same. That the skin is permeable by gas is also well known, it having been shown by Bichat that if a limb be immersed in a putrid gas the latter will be absorbed by the skin, and by Aubert that the skin absorbs about the  $\frac{1}{180}$ th of the oxygen absorbed by the lungs. Admitting, then, that under certain circumstances the skin undoubtedly can absorb, it still remains undetermined to what extent, under normal conditions, it does absorb. Covered, as the skin usually is in man, almost entirely with more or less clothing, it is difficult to comprehend how or what the skin under such circumstances can absorb, the gain in weight of the body through absorption of the watery vapor of the atmosphere sometimes instanced<sup>3</sup> being due to the absorption of the vapor by the lungs rather than by the skin. We have further seen that through the presence of the sebaceous matter the skin is rendered repellant of water, which thereby renders it very insusceptible to the taking up of foreign substances. Indeed, it is very questionable whether such are ever introduced into the system unless the epidermis be disintegrated, the view sometimes advanced<sup>4</sup> that substances are absorbed by the sweat ducts being very improbable, since the latter are already filled with sweat, and the movement of the sweat, being from below upward, would

<sup>1</sup> Madden : *Experimental Enquiry into the Physiology of Cutaneous Absorption*, p. 64. Edinb., 1838.

<sup>2</sup> Currie : *Medical Reports*, vol. i pp. 304-326. Watson : *Chemical Essays*, vol. iii. p. 100.

<sup>3</sup> Lining : *Phil. Trans.*, 1743, p. 496. Klapp : *Inaugural Essay on Cuticular Absorption*, p. 30. Philadelphia, 1805.

<sup>4</sup> Auspitz : *Wiener med. Jahrb.*, 1871. Neumann ; *Wiener med. Wochenschrift*, 1871.



tend to wash away foreign substances rather than favor their absorption. It would appear, therefore, as we pass from the lower to the higher animals, that the skin loses its significance as an absorbing surface, becoming essentially protective and excretory in function. Nevertheless, though the absorbing power of the skin in the economy of the higher animals may have been superseded by that of the lungs and alimentary canal, under certain conditions it may even in them act vicariously with the same, as no doubt it does, as regards the excretion of water by the kidneys as well as the lungs.

The skin acts not only as a general sensory surface through the impressions made upon the epidermis being transmitted thence to the more deeply situated cutaneous nerves, but through its tactile Pacinian and Krause corpuscles it is endowed with a special modification of sensibility—the tactile sensibility, or the sense of touch, by means of which we not only feel but appreciate to a certain extent the form, size, character or surface, weight, and temperature of objects. While the skin as a whole, therefore, is endowed with a general sensibility more or less acute in different parts of the body, its tactile sensibility, however, is restricted to certain portions of it, and most delicate in those situations where the corpuscles are most abundant. Thus, if the blunt but fine ends of a pair of dividers provided with a graduated bar, or the æsthesiometer, be applied to the tip of the tongue—the individual being blindfolded—the two ends of the dividers, though only separated by so much as the  $\frac{1}{4}$ th of an inch, will be appreciated as two distinct objects. If, however, the dividers be approximated until they are separated by less than that distance, the two impressions, a moment previous distinctly appreciated as such, now fade into one, as if but a single object was touching the tongue. Experimenting in this manner, it was first shown by Weber,<sup>1</sup> and afterward by Valentin,<sup>2</sup> that the sense of touch varies very much in different parts of the body, being most acute at the tip of the tongue and ends of the fingers; least so in the back, as shown in Table LXXIX.

TABLE LXXIX.<sup>3</sup>—TACTILE SENSIBILITY.

| Part of surfaces.                                    | Both points of dividers felt when separated by these distances. |
|------------------------------------------------------|-----------------------------------------------------------------|
| Tip of tongue . . . . .                              | 0.50 of a line.                                                 |
| Palmar surface of third phalanx of fingers . . . . . | 1.00 " "                                                        |
| " " " second " " " . . . . .                         | 2.00 " "                                                        |
| Dorsal " " third " " " . . . . .                     | 3.00 " "                                                        |
| Middle of dorsum of tongue . . . . .                 | 4.00 " "                                                        |
| End of the great toe . . . . .                       | 5.00 " "                                                        |
| Centre of hard palate . . . . .                      | 6.00 " "                                                        |
| Dorsal surface of first phalanx of fingers . . . . . | 7.00 " "                                                        |
| " " quarter of heads of metacarpal bones . . . . .   | 8.00 " "                                                        |
| Back of the heel . . . . .                           | 10.00 " "                                                       |
| Dorsum of the hand . . . . .                         | 14.00 " "                                                       |
| " " foot . . . . .                                   | 18.00 " "                                                       |
| Sternum . . . . .                                    | 20.00 " "                                                       |
| Five upper dorsal vertebræ . . . . .                 | 24.00 " "                                                       |
| Middle of " " " . . . . .                            | 30.00 " "                                                       |

When points of dividers are brought closer than these distances they are felt as one.

<sup>1</sup> Wagner : Physiologie, Band iii Zweite Abth. S. 524.

<sup>2</sup> Physiologie, Band ii. S. 558.

<sup>3</sup> Carpenter, article Touch, Cyclopædia of Anat. and Phys., vol. iv. part 2d, p. 1169.

It was also shown by Weber,<sup>1</sup> as a general rule, that differences in pressure and weight are appreciated most acutely by those parts of the skin which are most sensitive to the impressions of touch, as that of the fingers, for example, and that, while by the sense of pressure alone, a difference in weight of not less than one-eighth can only be determined by making a muscular effort, as well as in lifting, a difference of one-sixteenth can be accurately appreciated. It may be mentioned in this connection, however, that the appreciation by the skin of the temperature of the surrounding atmosphere, or of bodies applied to it, does not appear to depend upon nerves other than those of general sensibility, or that the fact of our appreciating the density, immobility, elasticity, etc., offered by bodies that we grasp or tread upon, or which, through their weight, offer a resistance to the exercise of muscular power, implies the existence of a special muscular sense. The ataxic symptoms present in certain cases of paralysis, often referred to as proof of the existence of a special muscular sense normally, are perfectly well accounted for by the loss of general sensibility. Since the impression made by the foreign body, whether it be the ground we tread upon or the child we hold in our arms, not being transmitted to the encephalon, in such cases it will not be reflected consciously or otherwise to the appropriate muscles whose action enables us to stand securely or grasp firmly, hence our inability to walk upon the ground or hold a child in our arms unless we look at the one or the other, the essential reflex action being then effected by the eye and optic nerve instead of the skin and cutaneous nerves.

The sense of touch, like the other senses, can be very much improved by attention and practice. Thus, it is said<sup>2</sup> that the female silk throwsters of Bengal can distinguish twenty different degrees of fineness in the unwound cocoons by the touch alone, and that the Indian muslin weaver makes the finest cambric with a loom of such simple construction that, if worked by the hands of a European, would turn out but little better than canvas. It is also a well-known fact, that those persons who are employed in mints, etc., in the daily habit of handling coins, detect at once, and with certainty, a light piece. As might be expected, the sense of touch is very much developed in those who have lost the sense of sight, or who have been blind. One of the most remarkable of such cases is that of Giovanni Gonelli, who, at twenty years of age lost his sight, but who, nevertheless, after a lapse of ten years, developed a great talent as a sculptor, modelling such an excellent statue out of clay of Cosmo de Medici from feeling one of marble that the Grand Duke of Tuscany sent him to Rome to make a statue of Pope Urban VIII., which was a very successful one, the likeness being said to be excellent. Stranger still, even a good knowledge of botany and conchology has been acquired through the sense of touch by persons who have been born blind, or who had lost their sight early in life. It is well known, also, as in the case of Baczko,<sup>3</sup> that the blind can learn to distinguish the colors of fabrics by the sense of touch.

<sup>1</sup> Weber, op. cit., Band iii., Zweite Abth. S. 543.

<sup>3</sup> Rudolphi: Physiologie, Band ii. S. 85.

<sup>2</sup> Carpenter, op. cit., p. 1177.



It is related that Sanderson, the blind professor of mathematics at Cambridge, could not only distinguish different medals, but could detect imitations of them often better than, professed connoisseurs, while his appreciation of variations of temperature, it may be mentioned also,<sup>1</sup> was so acute that he could tell, through slight modifications in the temperature of the air, when very slight clouds were passing over the sun's disk. It is a familiar fact, also, that the blind learn to read with great facility by passing their fingers over raised letters of about the size of those of a folio Bible. Terrible a calamity as the loss of sight is, it should not be forgotten, as the above examples teach us, what a delicate sense in that of touch we possess if cultivated, and that sources of pleasure and recreation through its development may be offered to those who are born blind, or who have lost their sight later in life.

<sup>1</sup> Dunglison : Physiology, vol. i. p. 697. Phila., 1856.

## CHAPTER XLVII.

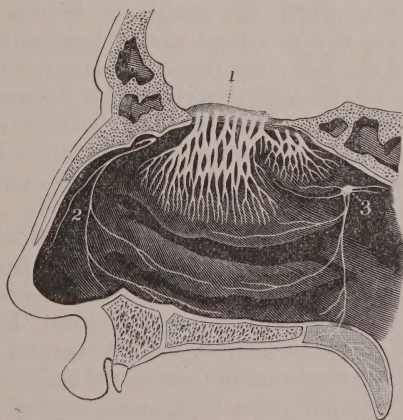
### THE NOSE AND OLFACTION. THE TONGUE AND GUSTATION.

JUST as we have seen that the skin, in addition to its other functions, acts as a general sensory organ, so we shall soon learn through the study of Development, that parts of it being especially modified become very susceptible to certain external impressions, and that such modifications, together with corresponding ones developed in the terminal nerves supplying the parts, constitute special sensory organs, such as the nose, tongue, eye; and ear, and inasmuch as, of such organs, the nose is the most simple in structure, we will begin the consideration of the special senses with the study of Olfaction.

#### OLFACTION.

The nose, the special organ of the sense of smell, is regarded anatomically as being limited to the pyramidal eminence of the face, extending from the forehead to the upper lip; physiologically, however, the nose—that is, the organ of olfaction—includes not only the parts just mentioned, consisting of the septum, cartilages, etc., but of the nasal cavities as

FIG. 446.



Distribution of nerves in the nasal passages. 1. Olfactory ganglion, with its nerves. 2. Nasal branch of fifth pair. 3. Spheno-palatine ganglion. (DALTON.)

well; the mucous membranes lining the latter being endowed not only with general sensibility, as we have seen, but with the special sense of olfaction, its upper half being supplied (Fig. 446) by the olfactory nerve, the special nerve of the sense of smell. The skin of the nose, thin

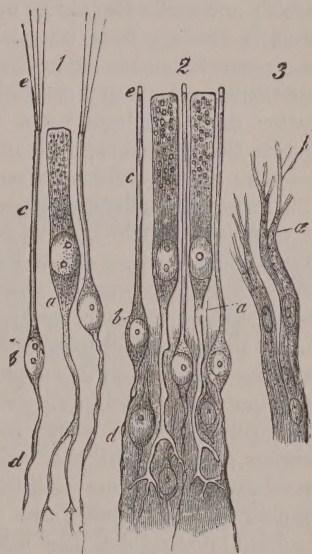


above but thick below, as elsewhere, is furnished with sudoriferous and sebaceous glands and hairs; the hairs are usually small except within the margin of the nostrils, in the latter position, however, they are well developed from all sides, and to a certain extent act like a fine sieve in keeping out dust, etc. The nasal cavities communicating with the exterior, in front, by the anterior nares, and with the pharynx, behind, by the posterior nares, are lined with a highly vascular mucous membrane, the Schneiderian or pituitary membrane closely applied to the adjacent periosteum and perichondrium, which becomes, at the nostrils, continuous with the skin, at the posterior nares with the mucous membrane of the pharynx, and at the lachrymo-nasal duct and lachrymal canals with the conjunctiva. The nasal mucous membrane varies very much as regards its thickness and vascularity. Thus upon the turbinated processes and turbinated bone it is very thick and vascular, and forming doublings at their inferior borders, and posterior extremities of the above, increases very much the extent of the nasal surface. Further, while the epithelium within the region of the external nostrils is of the squamous character, that lining the remaining portion of the nasal cavities is of the columnar kind, being non-ciliated, however, in the olfactory region, or that corresponding to the convex surface of the turbinated processes and the surface of the nasal plate of the ethmoid bone. The nasal mucous membrane is also provided with racemose glands whose secretion keeps the surface moist, a condition essential to the accurate perception of odoriferous impressions. The glands of the true olfactory membrane are, however, usually of a simpler character than those found in the remaining portion of the nasal mucous membrane. The special nerves of the sense of smell or the true olfactory nerves are given off as fifteen to eighteen filaments from the olfactory bulb to the olfactory region. The olfactory tract, of which the ganglionic bulb is the expansion, is usually described as the olfactory nerve, but improperly, since, as development shows, the olfactory tracts are outgrowths of the cerebral hemispheres, their morphological significance masked in man by the excessive development of the former. The olfactory tracts are two cords or bands, soft and friable, consisting of both white and gray nervous matter, which, passing forward and inward on the under surface of the anterior lobe of the cerebrum to the ethmoid bone, expand at the side of the crista galli into the olfactory bulbs, from which are given off, as just mentioned, the true olfactory nerves, which, passing through the cribriform foramina of the ethmoid bone, are distributed to the inner and outer walls of the upper parts of the nasal cavities. Each olfactory tract arises apparently by three roots, from the inferior and internal surface of the anterior lobe of the cerebrum in front of the anterior perforated space, the external and internal roots being composed of white matter, the middle of gray, the large proportion of the gray substance, one-third, entering into the composition of the olfactory tract, confirming what has just been said as to the true nature of the latter. While the anterior root can be traced into the middle lobe and the middle and internal roots into the anterior lobe, considerable obscurity still prevails as to the deep origin of all three roots. It would appear, however, that the long or external root originates in the island of Reil, the thalamus opticus

and the nucleus in the temporo-sphenoidal lobe in front of the hippocampus, the middle or gray root in the gray substance of the anterior perforated space, the inner root in the gyrus fornicatus. The true olfactory nerves, or the filaments given off from the olfactory bulb, as they descend from the cribriform plate ramify, and, uniting in a plexiform manner, spread out laterally in brush-like and flattened tufts (Fig. 486). In their minute structure, the olfactory differ from the ordinary cerebral and spinal nerves in being pale and finely granular, in not possessing a substance of Schwann, in adhering to one another, and in presenting oval corpuscles.

Their manner of termination is also peculiar, each olfactory fibre appearing to pass into the spindle-shaped bodies (*b*) interspersed between and among the epithelial cells (*a*) of the olfactory membrane (Fig. 447), which present a very characteristic appearance. These olfactory cells, so-called on account of their supposed function, present a very characteristic appearance, the central nucleated portion passing on the one hand internally into a beaded varicose-like thread (*d*) apparently continuous with the terminal olfactory fibril, and, on the other, externally into a rod-like structure (*e*), which in the frog is prolonged into fine hairs. That the olfactory cells, nerves, bulbs, and tracts constitute the essential structures by which external impressions are transmitted to the subiculum cornu of the hippocampal convolution in which the sense of smell is supposed to be localized, is proved by the harmonious results of experiments performed upon animals, of pathological cases observed in man, and of the facts of comparative anatomy. Thus, among the numerous experiments in which the olfactory tracts were divided, and the loss of the sense of smell noticed, may be mentioned those performed upon hunting dogs by Vulpian<sup>1</sup> and Philipaux, in which cases the animals, although deprived of food for thirty-six hours after complete recovery from the effects of the operation failed to find the cooked meat concealed in the corner of the laboratory. That destruction of the olfactory nerves, bulbs, or tracts in man due to disease or injury involves the impairment or loss of the sense of smell is well known to pathologists, a number of such cases

Fig. 447.



Cells and terminal nerve-fibres of the olfactory region highly magnified. 1, from the frog; 2, from man; *a*, epithelial cell, extending deeply into a ramified process; *b*, olfactory cells; *c*, their peripheral rods; *e*, their extremities, seen in 1 to be prolonged into fine hairs; *d*, their central filaments; 3, olfactory nerve-fibres from the dog; *a*, the division into fine fibrillae. (FREY after SCHULTZE.)

<sup>1</sup> Leçons sur la physiologie générale et comparée du système nerveux, p. 882, note. Paris, 1866.



having been observed by Schneider, Rolpinck, Eschricht, Fahner, Valentin, Rosenmuller, Cœneti, Pressat,<sup>1</sup> Hare,<sup>2</sup> Notta,<sup>3</sup> Ogle,<sup>4</sup> Flint.<sup>5</sup> That the olfactory bulbs and nerves are the essential organs of the special sense of smell is still further shown by the fact that they are usually best developed in animals in which the sense of smell is most acute, being better developed, for example, in the mammalia than in the remaining vertebrates, while of the former class it is among those orders as in the carnivora, in which the sense of smell is very acute, that the olfactory region is most developed, in the dog, for example, in which the sense of smell, as well known, is very remarkable. The olfactory nerves, though readily impressed by odorous emanations, are but little affected by ordinary ones, while the olfactory tracts appear entirely insensible to the latter.<sup>6</sup> That the appreciation of odors or olfaction is due to the material emanations given off by odoriferous substances being carried by the inspired air to the terminal filaments of the olfactory nerves, the olfactory cells, is shown by the manner in which one sniffs the air in order to perceive an odor, and from the fact that if the air does not pass through the nostrils, as in occlusion of the posterior nares or in division of the trachea, the sense of smell is abolished. In every case where odorous emanations are perceived, the latter must impinge upon the olfactory membrane, come in contact, excite the peripheral ends of the olfactory nerves. As a general rule, persons having offensive emanations from the respiratory organs are not aware of such, not appearing to be affected by odors passing from within outward through the nostrils. This is due, not so much to the odor being carried by the air expired through the nostrils instead of by that inspired, as to the fact that one becomes in time accustomed to such odors, and ceases to notice them, however fetid they may be. Like the sense of touch, and the other special senses, that of smell may be very much developed by practice; as exemplified in the discrimination of the quality of wine, drugs, etc. The sense of smell is, however, far more acute in the lower races of mankind than in the higher ones, to whatever extent in the latter it may have been developed by cultivation. Thus it is said that the Mincopies of the Andaman Islands scent the ripeness of the fruits; that the Peruvian Indians distinguish the different races of mankind by scent alone; that Arabs can smell a fire thirty miles off; that the North American Indians pursue by smell, their enemies or their game. However the sense of smell may be developed in man, it is far surpassed in acuteness by that of animals. Every sportsman is aware that odors are recognized by hunting dogs, to which he is entirely insensible.

The sense of smell is intimately related to that of taste, so much so, indeed, that if the nose be held, or plugged up, the characteristic taste of certain substances when swallowed, is not appreciated at all, as illustrated in drinking different kinds of wine, it being difficult, usually impossible, to distinguish the same under such circumstances. Further,

<sup>1</sup> Cited by Longet, *Anat. et Phys. du système nerveux*, tome ii. p. 38. Paris, 1842.

<sup>2</sup> *A View of the Structure, etc., of the Stomach and Alimentary Organs*, p. 145. London, 1821.

<sup>3</sup> *Archives générales de médecine*, p. 385. Paris, Avril, 1870.

<sup>4</sup> *Medico-Chirur. Trans.*, Lond., 2d ser. vol. xxxvii. p. 263. <sup>5</sup> Flint: *Physiology*, 1874, vol. v. p. 39.

<sup>6</sup> Magendie: *Journal de physiologie*, tome iv. p. 169. Paris, 1824.

it has been observed in those cases in which the sense of smell is lost, that of taste is usually lost also.

The influence exercised by the nose upon respiration has already been mentioned. We shall see, hereafter, that the nose, also, modifies very much the quality of the voice.

### THE TONGUE AND GUSTATION.

The sense of taste or gustation, enabling us to appreciate the savor of sapid substances when introduced into the mouth, is due to the susceptibility of the terminal filaments of the chorda tympani and glossopharyngeal nerves, of being impressed by contact of the same. The influence of the tongue in mastication and deglutition, the origin, distribution, and general functions of the chorda tympani and glossopharyngeal nerves, having been considered, it only remains for us now to point out the manner in which gustation is performed through the parts just mentioned. That the tongue is the organ of gustation there can be no doubt. It would appear, however, from experiments such as those performed by Longet<sup>1</sup> and others, in which different parts of the mucous membrane are touched with a sponge soaked in a sapid solution, that the sense of taste, probably in man at least, is limited to the dorsal surface of the tongue, and from the experiments of Camerer,<sup>2</sup> in which solutions were applied through fine glass tubes, more particularly to the circumvallate and fungiform papillæ, the parts around the latter not appearing to be impressed by sapid substances. The circumvallate papillæ (Fig. 448), so called on account of each papilla being surrounded by a trench or fossa, from seven to twelve in

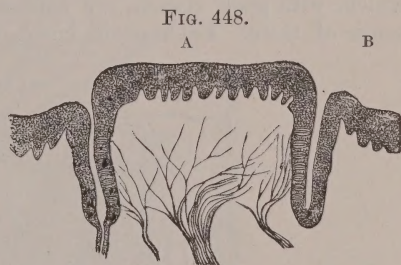


FIG. 448.  
A. The papilla. B. The surrounding wall. The figure shows the nerves of the papilla spreading toward the surface, and toward the taste-buds which are imbedded in the epithelium at the sides; in the sulcus on the left the duct of a gland is seen to open. (ENGELMANN)

number, are disposed in two rows, in the form of a reversed V on the back part of the tongue. Each papilla is covered by numerous small secondary papillæ, the latter, however, being concealed by the thick and stratified epithelium. The fungiform papillæ, more numerous than the circumvallate, and readily distinguished during life by their deep red color, while found in the middle and forepart of the dorsum of the tongue, are most numerous and closely set together at the apex and near the borders. Each fungiform papilla, while narrow at its attachment (Fig. 449), at its free extremity is blunt and rounded, and, like the circumvallate papillæ, is covered with secondary papillæ and epithelium, imbedded in the epithelium, and more particularly in that of

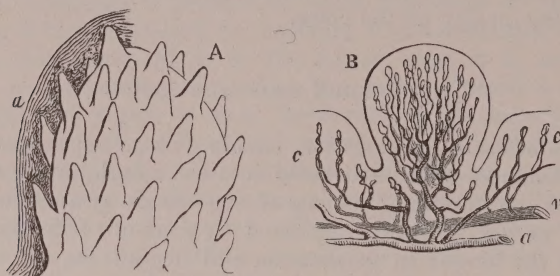
<sup>1</sup> Physiologie, tome iii. p. 52. Paris, 1873.

<sup>2</sup> Zeitschrift für Biologie, 1870, Band vi. S. 440.



the circumvallate papillæ, are found ovoidal flask-shaped bodies (Fig. 450), having a length of the  $\frac{1}{350}$ th of an inch, and a diameter of the

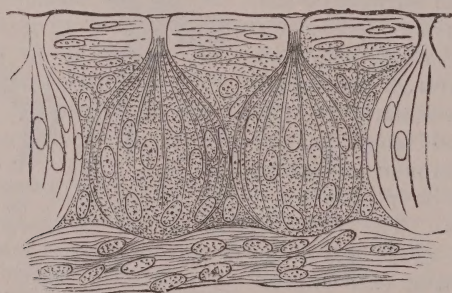
FIG. 449.



Surface and sectional view of a fungiform papilla. A. The surface of a fungiform papilla partially denuded of the epithelium. (35 diameters.) *p*. Secondary papillæ. *e*. Epithelium. B. Section of a fungiform papilla with the bloodvessels injected. *a*. Artery. *v*. Vein. *c*. Capillary loops of simple papillæ in the neighborhood, covered by the epithelium. *d*. Capillary loops of the secondary papillæ. *e*. Epithelium. (From KÖLLIKER, after TODD and BOWMAN.)

$\frac{1}{1600}$ th of an inch, consisting apparently of modified epithelial cells, which, with good reason, are supposed to be the special organs of the sense of taste. Each ovoid body, surrounded by flattened epithelial

FIG. 450.



Two taste-buds from the papilla foliata of the rabbit. 450 diameters. (ENGELMANN.)

cells, consists of a cortical and a central part, the former being composed of long, flattened, tapering cells, disposed edge to edge, and coming to a point at the taste-pore, the latter of spindle-shaped cells and taste cells, resembling very closely the olfactory cells; the distal end of the cell projecting from the orifice of the taste-bud, and the central beaded, varicose, and continuous with the terminal filament of the gustatory nerve. Such being the disposition of the taste cells, it would appear that the terminal filaments of the gustatory nerves, of which the former are the continuation, are excited by the flow of sapid solutions through the taste pore into the interior of the taste-bud; the taste cells being especially susceptible to impressions made by sapid substances, whence the impression is transmitted by the chorda tympani and glosso-pharyngeal nerves to the centres of taste localized in the

subiculum cornu of the hippocampus, when they are perceived. That the chorda tympani and the glosso-pharyngeal nerves are the special nerves of the sense of taste, the former more particularly for the anterior two-thirds of the tongue, the latter for the posterior third, can be shown, as already mentioned, both by experiments performed upon animals, and by pathological cases observed in man, division or disease of these nerves involving loss of the sense of taste. The glosso-pharyngeal differs from the chorda tympani, however, in this respect, in that it is a nerve of general sensibility, as well as that of taste, the chorda tympani (gustatory fibres) being a nerve of taste alone, the sensory fibres of the lingual nerve bearing to the chorda tympani the same relation that the sensory fibres of the glosso-pharyngeal bear to its gustatory ones. In conclusion, it may be mentioned, and as might be expected, that since at the anterior two-thirds of the tongue the fungiform papillæ are supplied by the chorda tympani at the posterior third, and the circumvallate papillæ by the glosso-pharyngeal, the taste of a substance might be different as it was placed upon the anterior or pos-

FIG. 451.



terior part of the tongue. Such has been experimentally found to be the case; thus, according to Lussana,<sup>1</sup> potassium chloride tastes cool and

<sup>1</sup> Archives de Physiologie, tome ii, p. 208. Paris, 1869.



saltish at the anterior part of the tongue, and sweetish at the posterior part; potassium nitrate cool and piquant at the anterior, and bitter and insipid at the posterior end. Certain substances, like mineral acids, ferric sulphate, jalap, and colocynth, while but little appreciated at the anterior part of the tongue, are appreciated very acutely at the posterior portion. On the other hand, meats, milk, and wines, are equally well appreciated at both ends of the tongue. It may be mentioned, incidentally, that the filiform papillæ the minute conical eminences densely set over the greater part of the dorsum of the tongue and disposed in lines diverging from the raphe, are tactile in function.

## CHAPTER XLVIII.

### THE EYE AND VISION.

THE organ of vision includes the optic nerve, the eye, and its appendages. The optic nerves—consisting of medullated, together with some gray nerve fibres—are usually described as arising from the optic chiasma, or commissure. Regarded, however, as the continuation of the optic tracts, the optic nerves in reality arise, as we have seen, from the optic lobes, and to a certain extent also from the thalami optici, corpora geniculata, cerebral peduncles, and tuber cinereum; the root fibres from these different points of origin, converging form flattened bands, which, winding obliquely around the under surface of the crura cerebri, cross each other to pass to the opposite eyes, the decussation of the nerves, or tracts, which, we have seen, is complete giving rise to the chiasma. It should be mentioned, however, that the fibres constituting the anterior portion of the chiasma are not derived from the optic tracts, but simply pass from one eye to the other, while the fibres constituting the posterior part—and sometimes wanting—pass from tract to tract without being connected with the eyes. The optic nerves proper, arising from the anterior and outer border of the chiasma, curved in direction and rounded in form, enclosed in a double fibrous sheath, derived from the dura mater and arachnoid, pass into the orbit through the optic foramina, piercing the sclerotic coat of the eye at its posterior, inferior, and internal portions; the thin, but strong membrane through which the nervous filaments pass into the sclerotic, known as the lamina cribrosa, being partly derived from the sclerotic, and partly from the coverings of the nerve fibres which are lost at this point. At about one-third or one-fourth of an inch behind the globe of the eye, the optic nerve receives the central artery and vein of the retina, which, together with a delicate filament from the ophthalmic ganglion, is thence transmitted within the centre of the nerve by a minute canal, lined with fibrous tissue. That the optic nerves are the special nerves of the sense of sight there can be no doubt, since their injury or division always involves impairment or loss of sight. While the optic nerves are the avenues or paths by which the impressions due to the presence of light are transmitted to the optic lobes and angular gyri, there to become, as we have seen, conscious, intelligent vision, they are, however, absolutely insensible to ordinary impressions. Not only have these nerves been pinched, cut, and cauterized in animals, without the latter evincing any pain, but their insensibility in man has often been observed also, as in surgical operations, for example, in which the nerves have been exposed. That the optic nerves are especially susceptible to the impressions of the rays of light is still further shown from the fact of their excitation, however caused, always giving rise in consciousness to



the idea of light—a severe blow on the orbit making one see stars, as often said, the mind having associated so uniformly the excitement of the optic nerve with the presence of light, that in time it becomes impossible to disassociate the two; the presence of the one invariably suggesting that of the other.

### THE EYEBALL.

The eyeball, a spheroidal body, partly imbedded in a cushion of fat, protected by the surrounding bony orbit and the eyelids, moistened by the lachrymal secretion, and moved by various muscles, is composed of several coats, concentrically disposed, and enclosing several refractive media. Were it not for the fact of the cornea being set in the sclerotic, like a crystal into the rim of the face of a watch, the eyeball would present the form of a spheroid. Owing, however, to the cornea constituting one-tenth of the outer circumference of the eye, and to the fact just mentioned, the longest diameter is in the antero-posterior direction, as may be seen from the results obtained by Sappey (Table LXXX.).

TABLE LXXX.<sup>1</sup>—DIAMETER OF EYEBALL IN FRACTIONS OF AN INCH.

|                                                   | Ant. post. | Transverse. | Vertical. | Oblique. |
|---------------------------------------------------|------------|-------------|-----------|----------|
| Mean of 12 females from<br>18 to 81 years of age, | 0.941      | 0.911       | 0.905     | 0.937    |
| Mean of 14 males from<br>20 to 79 years of age,   | 0.968      | 0.941       | 0.925     | 0.949    |

It will be observed, from the above Table, that all the diameters are less in the female than in the male. It may be appropriately mentioned in this connection, also, that all such measurements should be made as soon as possible after death, within from one to four hours, owing to the eyeball losing so soon its normal form and dimensions.

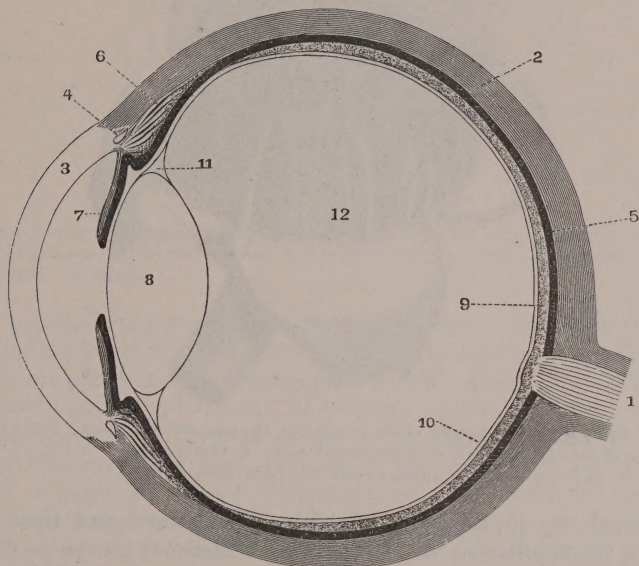
### THE SCLEROTIC AND CORNEA.

The sclerotic (Fig. 452, 2), the outer protective coat of the eyeball, covering the posterior five-sixths of the latter, varying in thickness from the  $\frac{1}{25}$ th to the  $\frac{1}{50}$ th of an inch, is a dense white, opaque tunic, composed of ordinary connective tissue, mixed with small elastic fibres and a few bloodvessels, and yielding, on boiling, gelatine. The cornea, the first of the refractive media, constituting the anterior sixth of the outer circumference of the eyeball, and varying in thickness from the  $\frac{1}{2}$ d to the  $\frac{3}{2}$ d of an inch, is the transparent projecting tunic (Fig. 452, 3,) attached to the periphery of the sclerotic, of which, indeed, it may be regarded as the continuation, consisting, like the latter, of layers of connective tissue, though somewhat modified, both structurally and chemically, since it is transparent, admitting light into the interior of the eye, and yielding chondrine on boiling. The cornea may be described as consisting of three parts: a stratified epithelium anteriorly, continuous with that of the conjunctiva, a middle portion,

<sup>1</sup> *Traite d'Anatomie*, tome troisieme, p. 747. Paris, 1877.

the cornea proper, continuous with the sclerotic, consisting of modified connective tissue, posteriorly, of a homogeneous, elastic lamella, covered with epithelium-like cells, the membrane of Demours or Descemet, the part of the membrane passing to the anterior surface of the iris, more noticeable in the eyes of the sheep and ox than in man, being known as the ligamentum pectinatum iridis. In a state of health in the adult, ves-

FIG. 452.



Horizontal section of the right eyeball. 1. Optic nerve. 2. Sclerotic coat. 3. Cornea. 4. Canal of Schlemm. 5. Choroid coat. 6. Ciliary muscle. 7. Iris. 8. Crystalline lens. 9. Retina. 10. Hyaloid membrane. 11. Canal of Petit. 12. Vitreous body. 13. Aqueous humor. (DALTON.)

sels are not found in the cornea, except at its circumference, where they are disposed in capillary loops, nutrition apparently being carried on by means of the corneal corpuscles. The nerves of the cornea are, however, very numerous, and are derived from the long and short ciliary nerves. Entering the sclerotic, and crossing the choroid, they pass into the cornea, extending almost through to its free surface.

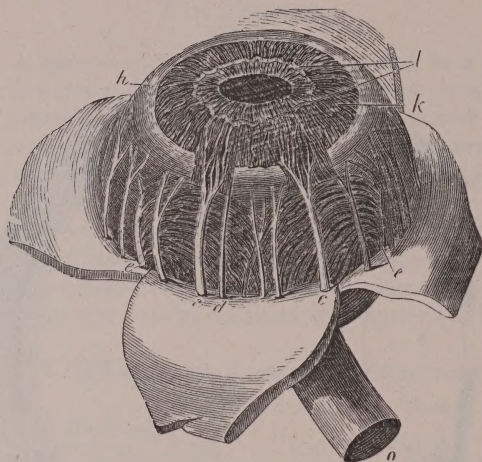
### THE CHOROID.

Removing the sclerotic in the manner represented in Fig. 453, the second coat of the eyeball from without inward, the choroid with its anterior prolongation, the ciliary muscle will then be exposed. The choroid may be regarded essentially as the vascular pigmental tunic of the eyeball; its inner or pigmental layer in reality, however, constitutes the outer coat of the retina, being developed, as we shall see hereafter, like the latter from the invaginated portion of the optic vesicle. The choroid, varying in thickness from the  $\frac{1}{150}$ th to the  $\frac{1}{25}$ th of an inch, and covering the eyeball to the same extent as the sclerotic, is connected by



its outer surface with the latter tunic by connective tissues, vessels, and nerves, the so-called *membrana fusca*, and, like the sclerotic, is traversed posteriorly by the optic nerve. The arteries of the choroid, the short ciliary, comparatively large after piercing the sclerotic close to the optic

FIG. 453.



Choroid membrane and iris exposed by the removal of the sclerotic and cornea. Twice the natural size. *a.* One of the segments of the sclerotic thrown back. *b.* Ciliary muscle. *c.* Iris. *e.* One of the ciliary nerves. *f.* One of the vasa vorticosa or choroidal veins. (QUAIN.)

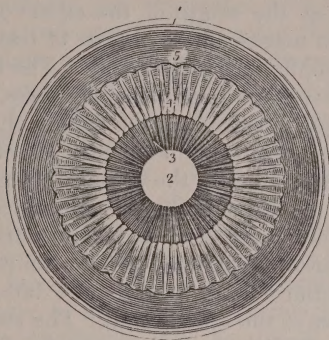
nerve, break up into branches, which pass forward and then inward to end in the capillaries, the latter being sometimes known as the tunic of Ruysch. The veins situated externally to the other vessels are very numerous, and, being disposed in curves converging into four trunks, present a peculiar appearance, which has given rise to the name of vasa vorticosa. Among the vessels of the choroid are also found elongated and stellated pigment cells, with branches, which, intercommunicating, constitute a sort of network. The nerves supplying the choroid are derived from the long and short ciliary. The inner surface of the choroid is smooth and is covered with the hexagonal pigmental cells of the retina, which will be considered as the outer layer of the tunic rather than, as formerly, as the inner layer or tapetum nigrum of the choroid for the reason just given.

#### CILIARY PROCESSES.

It will be observed from Fig. 453 that the choroid passes forward into the ciliary muscle, the latter in turn passing into the iris, constituting, in fact, one continuous layer—the second tunic of the eyeball. If, however, the choroid be viewed from behind, as represented in Fig. 454, in which the eyeball is supposed to have been divided transversely, it will be seen that the choroid passes forward and posteriorly into the ciliary processes, just as we have seen it passes forward but anteriorly into the ciliary muscle. Or, briefly, the relation of the parts may be

expressed by saying that the choroid splits at its anterior termination into the ciliary muscle in front, and the ciliary processes behind, the

FIG. 454.



Ciliary processes as seen from behind. 1. Posterior surface of the iris, with the sphincter muscle of the pupil. 2. Anterior part of the choroid coat. 3. One of the ciliary processes, of which about seventy-one are represented.  $\frac{1}{2}$ . (QUAIN.)

ciliary muscle being continued into the iris, hence the general term of uvea applied to all of these parts by the older anatomists. The ciliary processes or plications, about seventy in number, disposed radially behind the ciliary muscle and the iris, and fitting posteriorly, as we shall see, into corresponding plications of the suspensory ligament of the lens, more particularly into that part of it known as the zone of Zinn, consists of large and small thickenings of the choroid, the small folds alternating, though irregularly, with the large ones, the latter measuring about the  $\frac{1}{10}$ th of an inch in length and the  $\frac{1}{40}$ th in depth, and composed like the choroid proper of vessels and pigment, the latter, though, being absent in the rounded inner ends.

### CILIARY MUSCLE.

The ciliary muscle (Fig. 453, *b*), the continuation anteriorly of the choroid, about the  $\frac{1}{8}$ th of an inch wide, consisting of longitudinal and circular fibres, the latter, however, present at the periphery of the iris only, may be regarded as arising from the inner side of the junction of the sclerotic and cornea, close to the canal of Schlemm, and inserted into the choroid opposite the ciliary processes. Such being its disposition, it is evident that, in contracting, the nerves supplying it being the long and short ciliary nerves, will draw the choroid forward, thereby compressing the vitreous humor and relaxing the suspensory ligament of the crystalline lens, the significance of which action will be better appreciated when the subject of accommodation has been considered.

### THE IRIS.

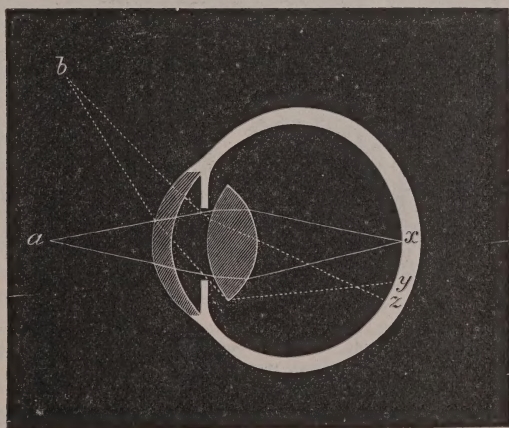
The iris (Fig. 453, *c*), the circular, contractile, and colored membrane seen through the transparent cornea, to which the characteristic



color of the eye is due, is the muscular diaphragm of the eye, the aperture in its centre or pupil permitting and regulating the passage of light into the interior of the eye. The iris, about as thick as the choroid, is attached by its circumferential border to the line of junction of the cornea and sclerotic at the origin of the ciliary muscle, and measures about one-half an inch across, and in a state of rest about the one-fifth of an inch from the circumference to the pupil. The iris consists essentially of a stroma of connective tissue and muscular fibres, the latter, disposed as a ring around the pupil, constituting the sphincter, and as rays from the centre to the circumference, the dilator muscles, of the iris. The pupil, or aperture in the iris regulating the amount of light admitted, varies in size according as the muscular fibres are contracted or relaxed, from the one-twentieth to the one-third of an inch, and during foetal life is closed by a delicate transparent membrane. The iris is supplied by the two long ciliary and anterior ciliary arteries, the latter being derived from the muscular branches of the ophthalmic. The two long ciliary arteries having pierced the sclerotic, one on each side of the optic nerve, pass between the latter tunic and the choroid to the ciliary muscle, and each vessel, just before reaching the iris, divides into an upper and lower branch, which, anastomosing with the corresponding vessels of the opposite side, and with the anterior ciliary arteries, forms a vascular ring, the *circulus major* of the ciliary muscle, from which small branches are given off, some of which supply the muscle, while others, converging toward the pupil, from a second vascular circle—the *circulus minor*; from the latter capillaries are given off which terminate in veins. The veins of the iris terminate in the circular venous sinus known as the canal of Schlemm, situated at the junction of the cornea with the sclerotic. The nerves of the iris are the long ciliary, which, as we have already seen, are given off from the nasal branch of the ophthalmic and the short ciliary nerves derived from the ciliary ganglion. The ciliary nerves, after piercing the sclerotic, pass forward on the surface of the choroid, to which tunic they give branches, to the ciliary muscle, in which they form a plexus continued forward into the iris; they apparently terminate at the pupil in a plexus of non-medullated fibres. It has already been mentioned that the fibres of the third pair of nerves and of the sympathetic exercise an antagonistic influence upon the pupil; division of the third pair being followed by dilatation, and that of the sympathetic by contraction of the pupil; and that the ciliary ganglion giving off the ciliary nerves supplying the muscular fibres of the iris, is made up to a considerable extent of fibres derived from the third pair and sympathetic. Putting together these facts, and further supposing that the fibres of the third pair and sympathetic pass through the ganglion, thence, as the ciliary nerves, to terminate in the circular and dilator fibres of the iris respectively, it becomes evident why the pupil dilates if the third pair be divided, since there is nothing then to antagonize the dilating effect of the sympathetic, and why the pupil contracts if the sympathetic be divided, since then there is nothing to antagonize the constricting effect of the third pair. Inasmuch, however, as the nasal branch of the ophthalmic contributes, as we have seen,

to the formation of the ciliary ganglion, the only question about which there can still be any doubt, is as to whether the sympathetic fibres passing to the ganglion of Gasser and thence to the nasal branch of the ophthalmic, influence the radiating fibres of the iris in the same manner as those of the sympathetic, just contrasted with the fibres of the third pair. Now, while it is very possible that some of the fibres of the nasal branch of the ophthalmic passing into the ciliary ganglion are derived from the sympathetic and influence the radiating fibres of the iris, it is probable that most of its fibres are derived from the ophthalmic, and endow, through the short ciliary nerves, together with the long ciliary, the iris and cornea with sensibility. We shall see presently that in the accommodating of the eye for near objects, and in the converging of the axes of the eyes for the same purpose, that the pupil is contracted, and that such is the case when the eye is exposed to a bright light, the pupil being widely dilated, however, when the light is dim. If what has just been said with reference to the influence of the third pair of nerves be accepted, it becomes intelligible why the pupil contracts under the stimulus of light, since the impression made upon the retina by the light being transmitted by the optic nerve to the optic lobe is thence reflected by the third pair to the circular fibres of the iris, causing the latter to contract the pupil. If such be the reflex mechanism, then the pupil should be uninfluenced by light if either the optic or third pair of nerves be divided, and such has been experimentally shown to be the case. It should be mentioned, however, that light, apart from any nervous influence, will exercise a direct stimulating effect upon the iris, causing the pupil to contract even after the eye has been removed from the orbit several hours after death. In connection with the influence

FIG. 455.



Diagrammatic section of the eyeball, showing difference of refraction for direct and indirect vision. *a, x*. Rays from a point in the line of direct vision, focussed at the retina. *b, y, z*. Rays from a point outside the line of direct vision, brought to a focus and dispersed before reaching the retina. (DALTON.)

exerted by the third pair of nerves upon the iris, this fact is an important one, since it offers an explanation of the pupil contracting even

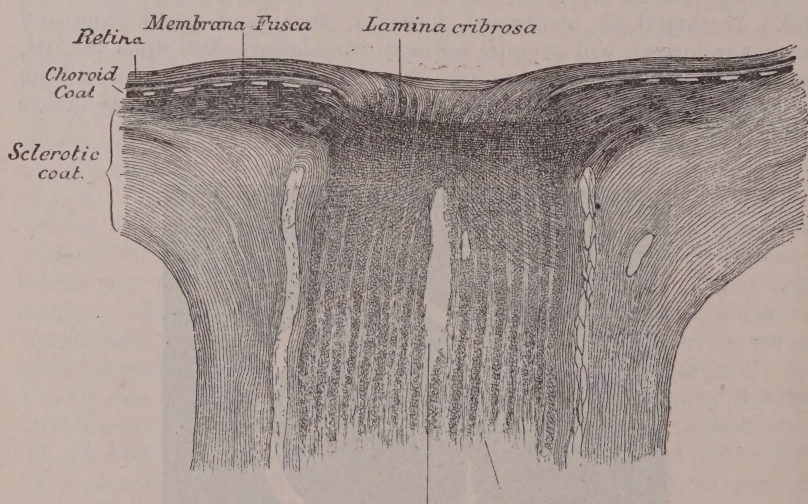


after division of the third pair. The contraction of the pupil in response to the direct stimulus of light is, however, very different from that observed when the action is a nervous, reflex one, taking place very slowly and requiring a long exposure. It need hardly be mentioned that section or electrical stimulation of the nerves supplying the iris, involving as they do sympathetic fibres, must modify the vascularity of the iris. Indeed, it has been held that contraction of the pupil is due to a congestion of the vessels, dilatation to a depletion of the same; the change in the diameter of the pupil is, however, too great to be accounted for in that way. While the function of the iris is without doubt that of a diaphragm, regulating, through the pupil, the amount of light admitted to the interior of the eye, it will be observed, from Fig. 455, that not only will the light enter the eye from a point (*a*) in the line of direct vision, but from a point (*b*) outside that line, and that the latter rays being brought too soon to a focus, are dispersed again before reaching the retina, and so give rise to confused vision.

### THE RETINA.

If the choroid, including the tapetum nigrum, be removed under water in the same manner as the sclerotic, the third tunic of the eye

FIG. 456.

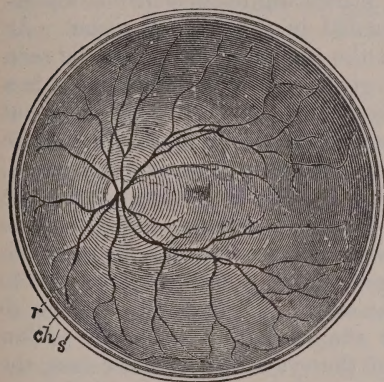


Section through the middle of the optic nerve and the tunics of the eye at the place of its passage through them. (ECKER.)

from without inward, or the retina, will be then exposed as a very delicate and transparent membrane, through which will be seen the posterior portion of the underlying vitreous humor. Within a short time after death, however, the retina loses its transparency and becomes opaline, the change being hastened by the action of water, alcohol,

and other fluids. The retina, varying in thickness from the  $\frac{1}{50}$ th to the  $\frac{1}{200}$ th of an inch, extends over the posterior portion of the eyeball to within a distance of about the  $\frac{1}{15}$ th of an inch of the ciliary processes, and, if torn from its anterior attachment, presents a finely indented edge, the so-called ora serrata. As a matter of fact, however, the retina

FIG. 457.



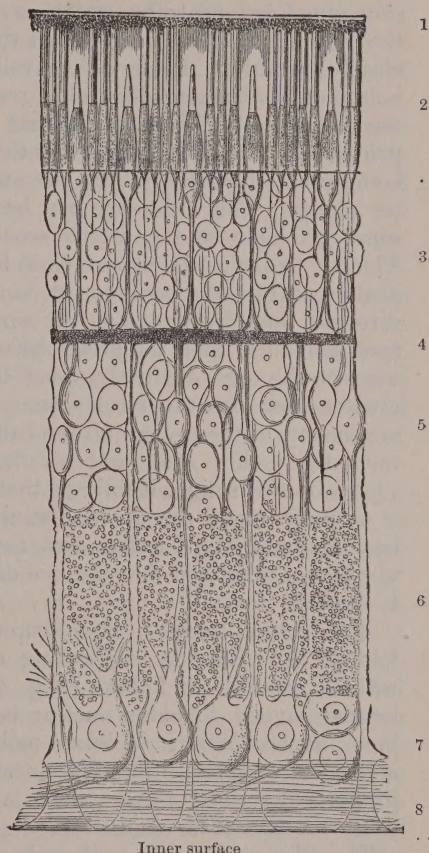
The posterior half of the retina of the left eye viewed from before. Twice its natural size. *s.* Cut edge of the sclerotic. *ch.* Choroid. *r.* Retina: in the interior at the middle the macula lutea with the depression of the fovea centralis is represented by a slight oval shade; toward the left side the light spot indicates the colliculus or eminence at the entrance of the optic nerve, from the centre of which the arteria centralis is seen sending its branches into the retina, leaving the part occupied by the macula comparatively free. (HENLE.)

does not terminate, as often said, at the ora serrata, but is continuous forward as a thin layer of transparent columnar nucleated cells, the pars ciliaris retinae, which, reaching the tips of the ciliary processes, then disappears. The retina, the nervous tunic of the eye, and that portion of it susceptible of being impressed by light, may be regarded as an expansion of the optic nerve, though it is usually described as being traversed by the latter, like the sclerotic and choroid.

The optic nerve apparently, then, penetrates the retina about the  $\frac{1}{8}$ th of an inch within, and the  $\frac{1}{25}$ th of an inch below the antero-posterior axis of the eye. The nerve fibres being at this point, the porus opticus, slightly elevated, give rise to a small eminence (Fig. 456), the colliculus

FIG. 458.

Outer or choroidal surface.



Inner surface

Diagrammatic section of the human retina. 1. Layer of the pigment cells. 2. Layer of rods and cones. . . Membrana limitans externa. 3. Outer nuclear layer. 4. Outer molecular layer. 5. Inner nuclear layer. 6. Inner molecular layer. 7. Layer of nerve cells. 8. Layer of nerve fibres. . . Membrana limitans interna. (SCHULTZE.)



nervi optici, between which the central artery of the retina appears, and spreads out arborescent-like, over the inner surface of the retina (Fig. 457), and the branches of the central veins converge and disappear. To the outer side of the optic nerve, about the  $\frac{1}{10}$ th of an inch, may be also seen on the inner surface of the retina, a yellow spot, somewhat elliptical in shape, about the  $\frac{1}{8}$ th of an inch long, and  $\frac{1}{36}$ th of an inch broad, its long diameter being horizontal, the so-called macula lutea or limbus luteus of Sömmering, presenting in its centre a depression, the fovea centralis, which is situated in the axis of vision. As the retina is so thin at this point that the pigmental layer can be seen clearly behind it, the fovea centralis gives the impression that it is a hole that has been made in the retina. It is an interesting fact, that the yellow spot of Sömmering has only been found in the eye of the primates. The sensitiveness of the retina to light varies very much, being greatest at the yellow spot, and gradually diminishing toward the periphery. The difference can be determined experimentally on the same principle as the tactile sensibility of the skin was determined. Thus, if two wires be placed close together, but sufficiently far apart to enable us to distinguish one from the other, and then the eye be so directed that the image of the wires shall fall, first upon the yellow spot, and then upon the great circle of the eye; in the latter case, the wires, to be seen distinctly, must be separated at a distance 150 times greater than in the former one. It is evident, therefore, why the movements of the eyeball all tend to bring the image of external objects upon the yellow spot, and as the latter only constitutes about, the  $\frac{1}{500}$ th of the retina, it follows that but a small portion of the latter is actually made use of in distinct vision. As an illustration, may be mentioned the familiar fact that, in reading, we see one or two words at a time, and that the eye must pass over the whole line in order to read it.

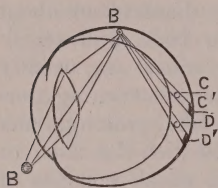
The retina consists, microscopically, of a connective tissue scaffolding, so to speak, supporting eight distinct layers disposed from without inward, as follows (Fig. 458): 1, pigmentary layer; 2, columnar layer; 3, outer nuclear layer; 4, outer molecular layer; 5, inner nuclear layer; 6, inner molecular layer; 7, ganglionic layer; and 8, nerve layer. The first outer, or pigmentary, layer of the retina, formerly described as the inner layer, or tapetum nigrum of the choroid, consists of a single stratum of hexagonal nucleated epithelium cells. The outer surface of each cell, that lying next to the choroid, is smooth, flattened, and usually free from pigment; the inner portion, prolonged as fine straight filamentous processes between the rods and cones of the second or columnar layer is, however, loaded with pigment. The second, or columnar layer, also known as the bacillary layer, Jacob's membrane, consists of millions of elongated bodies, the so-called rods and cones, disposed, in a palisade-like manner, between the pigmentary layer and the so-called membrana limitans externa, which is not a continuous membrane, but is formed through the connective tissue fibres of the retina, uniting more or less along a definite line at the boundary of the third, or outer nuclear layer.

The rods exceed the cones in number, there being usually about four rods to one cone, except at the macula lutea, where cones only are present; they have an elongated cylindrical form with a diameter of about  $\frac{1}{12500}$ th of an inch and a length of  $\frac{1}{500}$ th of an inch. The cones on the other hand, are shorter and thicker, having a diameter of about  $\frac{1}{4166}$ th of an inch, bulge out at the inner end or base, and terminate externally by a fine tapering portion. The cones are usually separated by a distance of  $\frac{1}{2500}$ th of an inch, the intervening portion being filled by rods. Through delicate fibre-like prolongations the inner ends of the rods and cones are connected with the third or outer layer of the retina, the outer nuclear layer, which consists of several strata of clear oval elliptical nucleated corpuscles or granules, from both ends of which delicate fibres are prolonged. These outer granules, presenting marked differences, are of two kinds, known as rod granules and cone granules, according as they are connected with the rods or cones, respectively. While the outer fibres of the outer nuclear layer are prolonged into the rods and cones, the inner fibres of the same are prolonged into the outer molecular layer; the latter in turn appears to be connected through fibrils with the granules of the inner nuclear layer, the latter being connected with the inner molecular layer. The seventh layer of the retina from without inward, the ganglionic or layer of nerve cells, consists of a stratum of nerve cells of a spheroidal or pyriform figure, which appears to be connected by fibres on the one hand, with the preceding inner molecule layer, and, on the other, with the fibres of the optic nerve. The latter, constituting the eighth layer of the retina, appears to be bounded by a distinct membrane, the *membrana limitans interna*, which, however, is not a continuous structure, as its appearance would lead one to suppose, but is formed, like that of the *membrana limitans externa*, by the terminal fibres of the sustentacular or connective tissue framework of the retina being united together at this point. From this necessarily brief description of the minute structure of the retina it will be seen that the layer of the rods and cones, or Jacob's membrane, bounded externally by the pigmentary layer, may be regarded as the termination of the optic nerve fibres. It has already been mentioned that at the macula lutea the rods are absent, the cones only being present; the latter are, further, much longer and narrower than elsewhere, especially opposite the fovea. At this portion of the retina the various layers of which it consists are also very much thinned. The yellow color of the macula, deepest at the centre, is due to a coloring matter diffused through all the layers except that of the cones and the outer nuclear layer. It might naturally be supposed that the anterior layer of the retina, that facing the light, would be the sensitive layer—as a matter of fact, of all the layers of the retina, however, that of the rods and cones is most sensitive to light, as can be shown experimentally by so illuminating the eye that one is able to perceive the shadows of the vessels of his own retina, which are cast upon the layer of rods and cones. The vessels of the retina being situated in its anterior layer, necessarily cast their shadows on one of its posterior layers, and the only reason that we do not ordinarily see these shadows is probably



that we have become so accustomed to them that they no longer attract our attention. If, however, the source of light be placed in an unusual position, as in Fig. 459, then the shadows of the

FIG. 459.



B, a candle placed at the side of the eye—that is, as much to the side of the centre of the cornea as possible. B', interior luminous source, formed by the rays of light concentrated by the crystalline lens upon the extreme lateral portion of the eye. CD, two vessels of the retina (the size of the retina is here greatly exaggerated). The shadow of these two vessels is seen as if projected at D' and C'. Experiment by PURKINJE.

the vessels falling on an unusual portion of the layer of rods and cones will be perceived, and will be seen by one looking at a very dark surface in a dark room, as if projected at D' C', and resembling exactly the vessels of the retina, the picture of the retina so seen being known as the vascular tree of Purkinje. Now it was shown by H. Muller,<sup>1</sup> that the distance between the anterior layer of the retina, and the layer of rods and cones, was about equal to that between the retinal vessels and their shadows; necessarily, then, the layer of rods and cones must be sensitive to light. Now, it being remembered that the layer of rods and cones lies next to the pigmental layer, and that the retina, with the exception of the latter layer, is transparent, it follows that a ray of light passes through the retina until it reaches the pigmental layer, when it ceases to be light, being transformed into either heat, chemical or nervous force; the latter exciting the rods and cones, gives rise to an impression which

is then transmitted back to the optic fibres on the anterior surface of the retina, where it is again reflected along the optic nerve fibres to the optic lobes, etc.

Beyond the statement that the rods and cones are excited by the heat or nerve force, or whatever the force may be into which the light is transformed in the pigmental layer, little can be said as to the special rôle they play in vision. Such facts, however, as that in the bat, hedgehog, and mole, nocturnal animals, and night birds, also, the retina consists solely of rods; whereas, in day-birds, especially in those which live on insects, of brilliant colors, the retina contains a much larger number of cones than the mammalia, would lead one to suppose that the rods are affected by differences in the intensity of the light, the cones by differences in its quality—that is, its color. While there can be no doubt that the fibres of the optic nerve transmit luminous impressions, or their modifications, in the manner described, it can be shown experimentally that the part of the retina where these fibres appear is insensitive to light, and is called, for that reason, the punctum cæcum. Thus, if two black points (Fig. 460, A, B), on a piece of paper, separ-

FIG. 460.



ated by a distance of two inches, be viewed at a distance of six inches by the right eye, the left eye being closed, the point B will be invisible, being then opposite the punctum cæcum, or blind spot.

## THE VITREOUS HUMOR AND HYALOID TUNIC.

The vitreous humor, while enclosed by the retina, does not, however, lie loosely in the cavity of the eyeball, being invested by a delicate membranous capsule, about the  $\frac{1}{8000}$ th of an inch in thickness—the hyaloid tunic. The latter is thicker in advance of the retina than elsewhere, and, as already mentioned, is impressed by the ciliary process of the choroid, the zone so formed around the crystalline lens, and well defined by the staining of the process, being known as the zone of Zinn. Anteriorly the hyaloid tunic splits into two laminae, which, diverging at the border of the crystalline lens, becomes confluent with the anterior and posterior surfaces of its capsule, the two laminae adhering at intervals; if the space between them be inflated, it will assume the appearance of a beaded canal, surrounding the circumference of the lens—the canal of Petit. Such being the disposition of the hyaloid tunic, it is evident that not only does it support the vitreous humor, through investing the latter, but acts also, from what has just been said, as the suspensory ligament of the lens. The vitreous humor, one of the refractory media of the eye, occupying about the posterior two-thirds of the globe, consists of a clear, glassy, gelatinous matter, divided into compartments by delicate membranous processes, which, given off by the hyaloid tunic, penetrate its substance. The specks that one sees occasionally floating about, as it were, in the field of vision, the so-called *muscae volitantes*, are due to the shadows cast upon the retina by the connective tissue elements suspended in the vitreous humor.

## THE CRYSTALLINE LENS.

The crystalline lens (Fig. 452, 8), the most important of the refracting media of the eye, transparent and very elastic, is situated in the hyaloid fossa of the vitreous humor, behind the pupil, and is enclosed, as already mentioned, between the laminae of the hyaloid tunic, the latter constituting its suspensory ligament. The crystalline lens is a double convex lens, the convexity of the anterior surface being greater than that of the posterior one, the antero-posterior diameter,  $\frac{1}{4}$ th of an inch, is, however, a little less than that of the lateral one,  $\frac{1}{3}$ d of an inch. With advance in age the convexities diminish, the lens becomes harder and inelastic, which accounts for the gradual diminution in the power of accommodating the eye to distances. If the lens be examined with a low magnifying power, there will be observed on each of its surfaces a star-like body, nine or sixteen rays of which extend from the centre to within about two-thirds of the periphery. The body of the stars and their rays are not of a fibrous character, like the rest of the lens, but consist of a homogeneous substance, which extends between the fibres. The latter are flattened, six-sided prisms, from the  $\frac{1}{4800}$ th to the  $\frac{1}{2400}$ th of an inch broad, and from the  $\frac{1}{13000}$ th to the  $\frac{1}{9000}$ th of an inch thick. Their flat surfaces are parallel with the surface of the lens, and their direction is from the centre, and from the rays of one star to the periphery, where they turn and pass toward those of the other. Chemically, the lens is composed of a nitrogenized substance, called crystal-



line, combined with inorganic salts. The crystalline lens is enclosed within a very thin, transparent, elastic membrane, the capsule, which is lined anteriorly with a layer of delicate nucleated cells.

#### THE AQUEOUS HUMOR.

The aqueous humor (Fig. 452, 13), the remaining of the refracting media of the eye, is a colorless, transparent, almost watery fluid, filling the anterior chamber of the eye—that is, the space between the cornea in front and the iris and crystalline lens behind, and the posterior chamber, or the space between the posterior surface of the iris and the lens, supposing that such a place exists, which is very doubtful, and in any case must be very small. That the aqueous humor is secreted possibly by the bloodvessels of the iris and ciliary processes, or the internal layer of the cornea, is shown by the rapidity with which it is reproduced after it has been evacuated, as in surgical operations performed upon the eye.

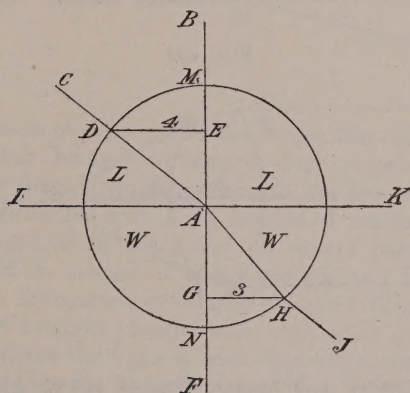
## CHAPTER XLIX.

### PHYSIOLOGICAL OPTICS.

#### REFRACTION AND ACCOMMODATION.

FROM the necessarily brief description just given of the eye, it is apparent that it resembles essentially in its structure the camera of the photographer, its refractive media being comparable to the lens, the iris to the diaphragm, the choroid to the internal blackened surface, the retina to the sensitive plate, the image of the external object being brought to a focus on the retina or sensitive plate respectively through the refraction undergone by the rays of light. In order, however, to understand the manner in which the rays of light are brought to a focus on the retina by the cornea, crystalline lens, etc., it will be necessary to describe briefly the phenomena of refraction in general, and the course that rays of light take in passing through refractive media. Suppose that *W W* (Fig. 461) represent a mass of

FIG. 461.



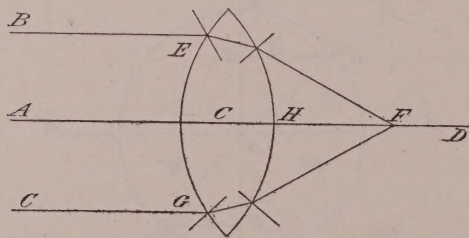
water, and *CA* the direction of the beam of light passing through the atmosphere *LL*, it will be observed that as the ray of light passes through the water it is bent toward the perpendicular *AF*, but that as it passes out of the water into the air again it is bent away from the perpendicular. Let now the line *CA*, representing the direction of the incident beam, be connected with the perpendicular *BF* by the line *DE*, and the line representing the refracted beam *AH*, be connected with the perpendicular by the parallel line *GH*, and it will be seen that the line *GH* is three-fourths as long as the line *DE*; and



further, that this ratio of 4 to 3, equal to 1.33 (more accurately 1.336), will be invariably the same whatever the angle may be that the incident beam  $CA$  makes with the surface of the water  $IK$ , except it be a right angle, the beam then passing directly through the water without being refracted at all.

If, however, with  $A$  as a centre, and a radius  $AD$ , a circle be described, the line  $DE$  becoming then trigonometrically the sine of the angle  $DAM$ , and the line  $GH$  the sine of the angle  $HAN$ , the law according to which light is refracted as it passes from air through water, may be expressed by saying that the ratio of the sines of the angles of incidence and of refraction is equal to 4 to 3, equal to 1.33, a constant for the particular substance water, or, briefly, that the index of refraction of water is 1.33. That is to say, if the line  $DE$  is 4 inches in length, then  $HG$  will be 3 inches, and so on, in the same ratio. If now, for water, crown glass be substituted, it will be found that the sine of the angle of incidence  $DE$  is to the sine of the angle of refraction  $HG$  not as 4 is to 3, as in the case of air and water, but as 3 to 2—that is, the index of refraction for the particular substance crown glass is 3 to 2, equal to 1.5. Bearing in mind then, that as the beam of light passes from the air through the glass it is bent toward the perpendicular, but away from it as it passes out of the glass, and that by the index of refraction is meant the ratio of the sines of the angles of incidence and refraction, there will be no difficulty in comprehending the manner in which the direction of a beam of light is altered in passing through biconvex and biconcave lenses. Let  $C$  (Fig. 462),

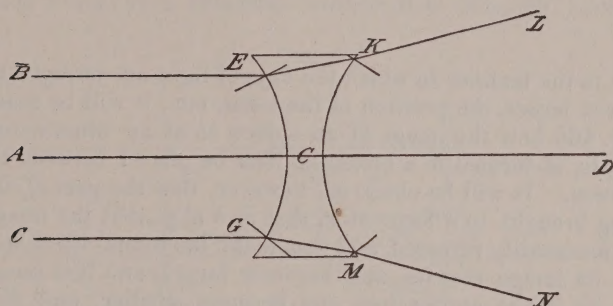
FIG. 462.



for example, represent a biconvex lens of crown glass in which the radii of curvature are nearly equal—that is to say, the two surfaces or curves of the lens are about equally distant from the centres of the circles of which these curves form parts, and that  $BE$ ,  $CG$  be two luminous rays parallel with the principal axis  $AD$  passing through the optical centre  $C$  of the lens, which fall upon the lens at the points  $E$  and  $G$ , respectively. Then, according to the law just enunciated, the ray  $BE$  being first bent toward the perpendicular, and then away from the perpendicular, and the ray  $CG$  being in the same manner bent first toward and then away from the perpendicular, and the ray  $AC$  being in the direction of the optical axis, and consequently passing through the lens perpendicularly, and, therefore, unrefracted,

it follows that the three rays, and all others parallel with them, will meet at a point  $F$ , known as the principal focus, and situated in the principal axis of the lens at a distance from the latter ( $FH$ ) which will be determined presently, and known as the principal focal distance. The effect of a biconvex lens is then to bring parallel rays of light to a focus on the side of the lens opposite to the source of light, the amount of convergence depending upon the radius of curvature to the lens and its index of refraction, which in this particular case, as we have seen, is 1.5. The converse of this is also true, since if the source of light be at the principal focus  $F$ , then the divergent rays after leaving the lens will be brought parallel with each other, and with the principal axis. Such being the action of a biconvex lens, it will be seen from a comparison of Fig. 462 with Fig. 463, that the action of a biconcave lens

FIG. 463.



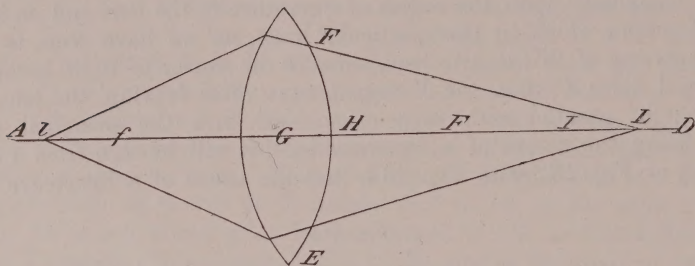
is exactly the opposite of a biconvex one, since the rays of light ( $BE$ ,  $CG$ , Fig. 463), after being bent toward their respective perpendiculars and then away from them, according to the law of refraction, will diverge from the principal axis  $AD$ , instead of converging toward it, and the rays of light  $BE$ ,  $CG$ , and all others parallel with them, diverged as  $KL$ ,  $MN$ , instead of being brought to a focus. The converse of this is also true, since it will be observed that the converging rays  $LK$ ,  $NM$  are brought parallel with each other on the side of the lens opposite that where the light is now supposed to be.

Let us now consider the case in which the luminous object  $L$  is beyond the principal focus  $F$  (Fig. 464), but so near that all the incident rays  $LE$ ,  $LF$  form a divergent cone, then, according to the law of refraction, the rays, after leaving the lens, will be found to come to a focus at  $l$ , and the converse of this will be found to be true, since, if the luminous object be placed at  $l$ , the focus will then be at  $L$ , hence  $l$  and  $L$  are conjugate foci. Further, it will be found by experimentation, or by calculation, that if the distance between the luminous object  $L$  (Fig. 464) and the lens be twice the focal distance—that is, twice  $HF$  equals  $HI$ —then the focus  $l$  will be situated on the other side of the lens at the same distance, or twice  $HF$ , as at the point  $A$ , on the axis  $AD$ ; if the distance between the lens and the luminous



object be less than twice the focal distance, the focus  $l$  will be situated beyond the point  $A$ , and if more than twice the focal distance, as at  $L$ , then the focus will be situated within the point  $A$ , as at  $l$ —that is, between the point  $A$  and the lens. After what has just been said, with

FIG. 464.



reference to the manner in which the rays of light are brought to a focus by biconvex lenses, the position of the focus, etc., it will be readily seen from Fig. 465 how the image of an object, as of an illuminated arrow, for example, is formed if a biconvex lens be placed between the latter and a screen. It will be observed, however, that the part of the arrow at  $a$  being brought to a focus at  $x$ , that at  $b$  at  $y$ , that the image of the arrow is necessarily reversed, and that if the luminous object approaches the lens its image recedes, and becomes larger, and if it recedes from the lens its image approaches, and becomes smaller, and that if the luminous object be situated at twice the focal distance from the lens, its image will be of the same size, and situated at the same distance from the lens. The distance at which the image is formed behind the lens can be readily calculated by the following formula:  $\frac{1}{b} = \frac{1}{f} - \frac{1}{l}$ , in which, in the distance of the image,  $f$  the local distance of the lens, and  $l$  the distance of the luminous object; thus, for example, suppose that  $f$  equals 6 cm.,  $l$  equals 24 cm., then  $\frac{1}{b} = \frac{1}{6} - \frac{1}{24} = \frac{1}{8}$  cm.—that is to

FIG. 465.

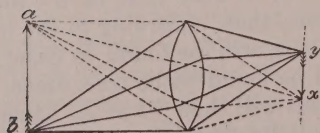
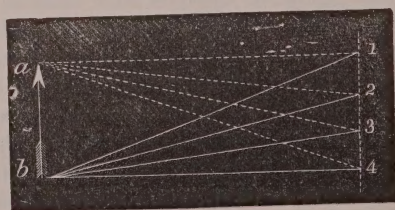


FIG. 466.

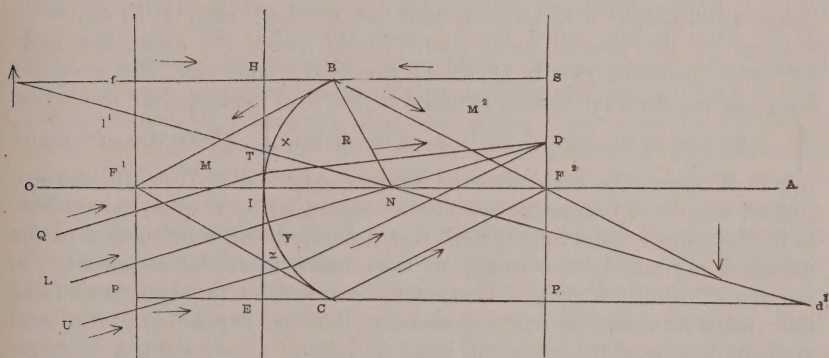


say, the image will be situated 8 cm. behind the lens. It need hardly be added, that in the absence of a lens, the rays of light will follow the

paths indicated in Fig. 466, and as the light from  $a$  will meet at 4 that from  $b$ , at  $l$  that from  $a$ , no image of the arrow will be formed upon the screen. Having considered now the properties of lenses, let us apply what has been established of the same to the elucidation of vision, and show how the rays of light, passing successively through the cornea, aqueous humor, crystalline lens, and vitreous humor are finally brought to a focus on the retina.

In considering the paths of the rays of light through the refractive media of the eye physicists make use of a normal schematic eye, a standard eye, so to speak, in which certain cardinal points have been established, and by which the rays of light through the eye can be readily constructed, the focus determined, and the size of the image estimated. Let us endeavor, then, to explain what is understood by the cardinal points, the use made of them in elucidating vision, and how they are determined. Let  $M, M^2$  be two refractive media separated from each other by a spherical surface  $BC$  (Fig. 467), constituting

FIG. 467.



what is known optically as a simple collecting system, and  $N$  the centre of curvature—that is, the centre of a circle, of which  $BC$  forms a part. All the radii drawn from the centre  $N$  to  $BC$ , such as  $NB, Nx, Ny$ , being perpendicular rays of light falling in the direction of the radii, must pass unrefracted through  $N$  as  $LD, I'd'$ , for example, and are called, therefore, lines of direction, while  $N$ , the point of intersection of all such lines, is called the nodal point. The line  $OA$ , connecting  $N$ , the centre of curvature, with the vertex  $I$ , and prolonged in both directions, is known as the optic axis, the plane  $HE$ , perpendicular to the optic axis at  $I$ , being called the principal plane, and the point  $I$ , within the latter, the principal point. Such being presupposed, it can be shown that all rays parallel with each other, and with the optic axis and the medium  $M$ , such as  $fH, pE$ , falling upon  $BC$ , come to a focus at  $F^2$  in the second medium, called the second principal focus, or second focal point, the plane  $SF^2P$ , perpendicular to the optic axis  $OA$ , at this point, being the second focal plane. Of course, the converse of the above is true—that is, rays diverging from  $F^2$ , such as



$F^2 B$ ,  $F^2 C$ , pass into the first medium parallel with each other, and with the optic axis. Further, it will be seen from an inspection of Fig. 507, that rays which are parallel to each other in the first medium, but not parallel with the optic axis, such as  $Q T$ ,  $U Z$ , come to a focus in the second medium in the point  $D$  of the second focal plane, where the non-refracted directive ray  $L D$  meets the latter, and that rays diverging from  $B$  pass through the first medium parallel with each other, but not parallel with the optic axis. It is also evident that all rays, which, in the second medium are parallel with each other, and with the optic axis, such as  $S B$ ,  $P C$ , come to a focus ( $F^1$ ) in the first medium, called the first focal point, or first principal focus, the plane of  $F^1 p$ , perpendicular to the optic axis at this point, being known as the first focal plane. Of course, the converse of the above is true, viz., that rays diverging from  $F^1$  pass through the second medium parallel with each other and with the optic axis.

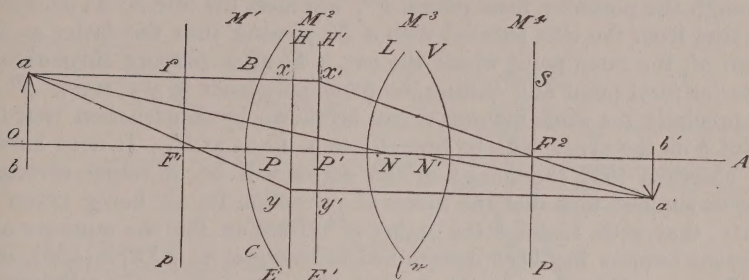
Finally it follows that the radius of the spherical surface  $N I$  is equal to the difference of the distance of the focal points  $F' F''$  from the principal point  $I$ —that is, that  $N I = F^2 I - F' I$ . Such being admitted, it will be seen that an incident ray ( $Q T$ ) comes to a focus in the second focal plane in the point  $D$ , where the non-refracted directive ray  $L D$  meets the latter, and that the reversed image of an external object, situated in the first medium like the arrow

↑ is formed in the second medium at the point ↓ where the prolonged ray  $B F^2$  meets the non-refracted directive ray  $L' D'$ . Now did the eye consist simply of two refractive media, separated by a spherical surface, as in the simple collecting system just described, the construction of the refracted ray and of the image of the object, would be essentially the same and equally simple. Inasmuch, however, as the eye consists of four refractive media, cornea, aqueous humor, crystalline lens, and vitreous humor, the cornea and aqueous humor constituting a concavo-convex lens, the crystalline a biconvex lens, and the vitreous humor a concavo-convex lens, to apply to the eye what has just been established would involve proceeding from medium to medium, which would be a tedious operation. If, however, the several media are centred, that is, if they have the same optic axis, which is pretty nearly the case in the eye, then as shown by Gauss,<sup>1</sup> the refractive indices of such a system may be represented by two equally strong refractive surfaces at a certain distance, the rays falling upon the first system not being refracted, but projected, so to speak, parallel with themselves to the second surface as at  $x x'$ ,  $y y'$ , refraction taking place at the latter just as if that surface alone was present, the only data required in determining the above, being the refractive indices of the media, the radii of the refractive surfaces, and the distances of the latter from each other, which, as we will show presently, can be experimentally determined. Let  $M^1$ ,  $M^2$ ,  $M^3$ , and  $M^4$  (Fig. 468) be four media for example, such as the air, aqueous humor, crystalline lens, and vitreous humor;  $B C$  a spherical surface like the cornea, separating the air from the aqueous humor;  $L l$

<sup>1</sup> Dioptrische Untersuchungen Abhand. Göttingen Gesells., 1841.

the anterior surface of a biconvex lens like the crystalline lens, a spherical surface separating the aqueous humor from the substance of the lens; and  $Vv$  the posterior surface of the lens, also a spherical surface, reversely disposed, however, with reference to the cornea and

FIG. 468.



anterior surface of the lens, and separating the substance of the lens from that of the vitreous humor. Such being the relation of the refractive media, and the spherical surfaces separating them, the cardinal points of such a system, six in number, as deduced from the radii of curvature, indices of refraction, etc., determined experimentally are as follows: two focal points ( $F' F^2$ ), two principal points ( $P P'$ ), two nodal points ( $N N'$ ). Inasmuch as the properties of the two foci  $F' F^2$ , as regards the rays of light diverging from or converging toward them respectively, and of the anterior and posterior focal planes  $f p$ ,  $S P$ , are essentially the same as already described and represented in Fig. 507, it will not be necessary to consider them again in detail in this connection. As regards the principal points  $P P'$  being in a transparent medium, their relation is such that a luminous point in the medium, appearing to an observer on the left to be owing to the refraction at  $P$ , to one on the right would appear to be at  $P'$ . That is to say,  $P P'$ , being conjugate foci like  $Ll$  (Fig. 464), rays of light passing through one point will pass through the other also;  $P P'$  being the principal points,  $H E$  and  $H' E'$  will be principal planes, and each point of the one plane having a conjugate focus in the other, a ray of light passing through a point on one plane will pass through a corresponding point on the other at the same distance from the axis, and on the same side, the distance  $F' P$  being the anterior focal length, and the distance  $F^2 P'$  the posterior focal length. In fact, either plane may be regarded as the image, the other being the object. It will be observed that the nodal points  $N N'$  are so disposed that if the incident ray  $a N$  were prolonged, it would emerge parallel with the emergent ray  $N' a'$ , and vice versa. In a simple lens, however, the optical centre being the only point through which a ray may pass and emerge parallel to its original direction, and all straight lines other than the principal axis passing through the optical centre being secondary axes, it follows that rays passing through the nodal points  $N N'$  may be regarded as secondary axes, and that these points represent the optical centres of the surfaces to which  $P P'$



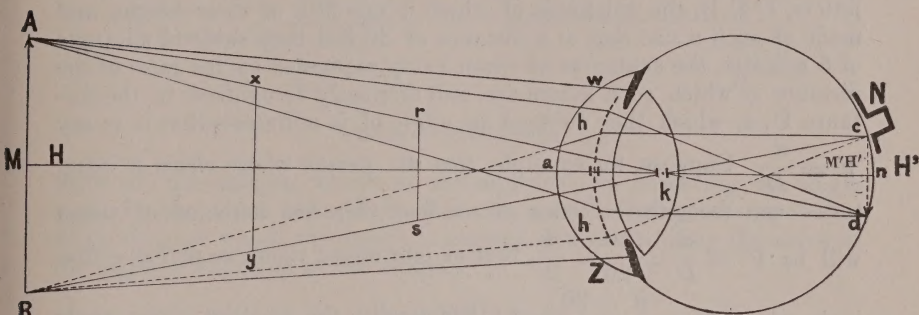
respectively belong. Such being the position of the cardinal points in the system of refractive media and spherical surfaces represented in Fig. 468, let  $ab$  be an object, an illuminated arrow for example, from which rays pass through the above; its image will be formed at  $b'a'$ . That this must be the case, can be at once shown by construction, for the ray  $af$ , after cutting the two principal planes  $rr'$ , and passing through the posterior focal points  $F'^2$ , will meet the line  $N'a'$ , emerging parallel from the lens parallel with  $aN$ , passing into the latter at the point  $a'$ , the same point where the ray  $aF'$  after passing through the anterior focal point and cutting the principal planes in  $yy'$  meets  $N'a'$ . In precisely the same manner it can be shown by construction that the point  $b$  of the arrow will be brought to a focus at  $b'$ . It need hardly be observed that the image of the arrow will be of course reversed. Let us suppose now that the index of refraction for air being taken as unity, that with Listing<sup>1</sup> the index of refraction for the aqueous and vitreous humors has been determined to be equal to 1.3379 ( $\frac{103}{77}$ ), that of the crystalline lens to be 1.4545 ( $\frac{16}{11}$ ), the radius of curvature of cornea 8 mm. ( $\frac{8}{25}$  of an inch), the radius of curvature of the anterior surface of the crystalline lens 10 mm., that of the posterior surface 6 mm., the distance of the anterior face of the cornea from the anterior surface of the crystalline lens to be equal to 4 mm., the distance from the anterior surface of the lens to the posterior surface, or the thickness of the lens, 4 mm., then by means of the appropriate formulæ, developed through the relations existing between the radii of curvature, the indices of refraction, etc., and the six cardinal points, the exact position of the latter in the human eye can be shown to be as follows:

The anterior principal focus 12.8326 mm. in front of the cornea, the posterior principal focus 22.6470 mm., the anterior principal point 2.1746 mm., the posterior principal point 2.5724 mm., the first nodal point 7.2420 mm., the second nodal point 7.6398 mm. behind the cornea. The distance between the anterior principal focus and the anterior principal point—that is, the anterior focal length being then 15.0072 mm. = 12.8326 + 2.1746, and the distance between the posterior principal focus and the posterior principal point—that is, the posterior focal length being 20.0746 mm. = 22.6470 — 2.5724, and the distance between the two principal points 0.3978 mm., and the nodal points 0.3978 mm. The two nodal points or principal points separated by only a distance of 0.39 mm. (about the  $\frac{1}{25}$  of an inch) may be regarded practically as coinciding, and we may assume, therefore, for the sake of simplicity, without introducing any very sensible error in the construction, that there is but one nodal or principal point, and therefore but one refractive surface for all the media of the eye. The eye so simplified, and constituting the so-called reduced eye of Listing, enables us to determine very readily the position and size of the inverted image of an external object formed upon the retina. Thus, for example, let  $AB$  (Fig. 469) represent an object placed vertically in front of the eye, then  $AD$ ,  $BC$ , being rays of direction and passing directly through the nodal point  $K$ ; unrefracted rays from  $A$  after refraction, will come to a focus on  $D$ , rays from  $B$  to

<sup>1</sup> Dioptrik des Auges. Wagner, Physiologie, Band iv. S. 451.

a focus at C, intermediate rays at some intermediate point (G). The rays of light taking this course through the media of the eye, the inverted image of the external object will be found on the retina at D C. Further, since in simple lenses the size of the image is to the size of the object as

FIG. 469.



the distance of the image from the lens is to the distance of the object from the lens, or, as in the case of the crystalline lens which we are now considering, as the distance of the image from the nodal point  $gk$  is to the distance of the object from the nodal point  $Mk$ , it follows that the size of the image

$$= \frac{\text{size of the object} \times \text{distance of image from nodal point}}{\text{distance of object from nodal point}}.$$

The distance of the image from the nodal point being, however, the posterior focal distance may be regarded as equal to the distance of the retina from the cornea ( $P'$ ), minus the distance of the nodal point from the cornea ( $R$ ), the distance of the object from the nodal point being equal to the distance of the object from the cornea ( $P$ ), plus the distance of the cornea from the nodal point ( $R$ ); such being admitted, the formula for the size of the image may be conveniently expressed as follows:

$$I = \frac{O \times P' - R}{P + R}.$$

Supposing that the object  $O$  be 1000 mm. high,  $P' = 22.6470$  mm.,  $R = 7.4$  mm.,  $P = 15.2396$  metres, then

$$I = \frac{1000 \times 15.247}{15.2396 + 7.4}.$$

That is to say, that the image of an object 1000 mm. (39.3 in.) in height seen at a distance of 15.2396 metres (50 feet) is 1 mm. ( $\frac{1}{25}$ th of an inch) in height, or a thousand times smaller. It will be observed also from Fig. 469 that the visual angle  $AkB$ —that is, the angle under which  $AB$  is seen—being the same as the angle under which the objects  $xy$ ,  $rs$ , are seen, that the image of all three objects formed on the retina must be the same, and that, therefore, the apparent size of all three objects, though differing in size, will be the same also. It is also

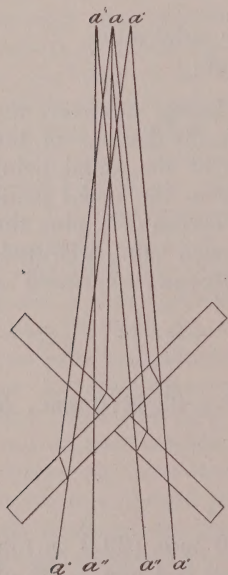


obvious that the size of the visual angle depends on the size of the object and distance of the latter from the eye. From the fact of the smaller the visual angle under which distinct vision is possible the more acute the vision, the latter is evidently inversely as the size of the visual angle. The measure of the acuteness of vision in general use among physiologists and ophthalmic surgeons, based upon this principle is a series of letters, C C B, the thickness of which is one-fifth of their height, and made of such a size that at a distance of 20 feet they subtend an angle of 5 minutes, the acuteness of vision being expressed by the ratio of the distance at which such letters are still distinctly recognized to the distance D, at which they subtend an angle of 5 minutes—that is to say

$V = \frac{d}{D}$ . Suppose, for example, that the person whose vision is being tested can recognize a letter at ten feet, then his acuteness of vision will be  $V = \frac{d}{D} = \frac{10}{20} = \frac{1}{2}$ , that of one whose vision is perfect—that

is, in whom  $V = \frac{d}{D} = \frac{20}{20} = 1$ . Practically, the smallest visual angle permitting distinct vision is about 60 seconds, and corresponding, as it does to a retinal image of about 0.004 mm., it will just about cover one of the cones of the retina. Two points seen under such a small visual angle would therefore appear as one. It has already been mentioned that the cardinal points, by means of which we follow the rays of light as they pass through the media of the eye and determine the position and size of the retinal image, are deduced from the indices of refraction of the aqueous and vitreous humors, lens, radius of curvature of cornea, etc., experimentally determined. Inasmuch as the methods by which the indices of refraction of the media of the eye are determined, are essentially the same as in the case of water or glass, and represented in Fig. 465, it need not in this connection be described again. The radius of curvature of the cornea and crystalline, however, being deduced by formulæ from the size of their reflected images, and the latter being measured by the ophthalmometer, the method of determination merits at least a brief description. The principle upon which the ophthalmometer, invented by Helmholtz,<sup>1</sup> is constructed is, that if an image of an object be viewed through two plano-parallel glass plates (Fig. 470) the image, through refraction, will appear double, and that if the plates be so approximated

FIG. 470.



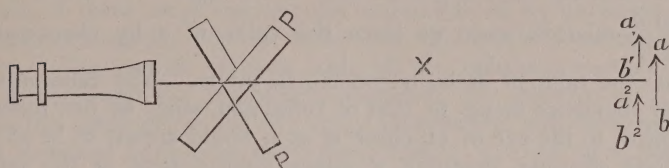
Object viewed through two glass plates.

that the inner edges of the two images are brought in contact, then the distance between the outer edges of the two images will be twice the size

<sup>1</sup> *Optique Physiologique Traduite*, by Juval et Klein, p. 11. Paris, 1867.

of the single image. To measure the size of an image by the ophthalmometer, it is only necessary, then, to determine the lateral displace-

FIG. 471.



Schema of ophthalmometer.

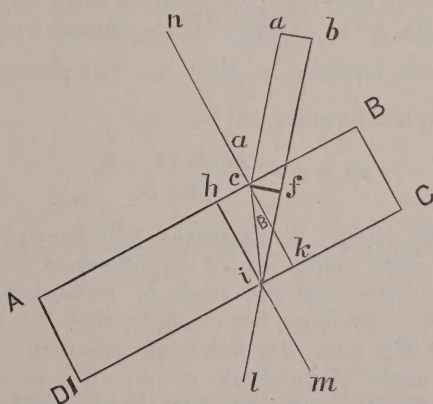
ment of the images, which is accomplished by observing the angle made by the glass plates  $PP$ , with the axis  $X$  of the telescope (Fig. 471), through which the image is viewed, and substituting the value of the angle so obtained in the formula

$$L = 2T \frac{\sin (\alpha - B)}{\cos B}$$

in which  $L$  = the lateral displacement,  $T$  = the thickness of the glass plates,  $\alpha$  = the angle of incidence,  $B$  = the angle of refraction.

The manner in which the above formula is developed, will become clear from a consideration of the relation of the parts involved, as represented in Fig. 472, in which, for simplicity,  $ABCD$  is one of

FIG. 472.

To illustrate the measurement of the lateral displacement,  $ab$ .

the plates of glass placed in front of the objective of the telescope, and  $ac$  the incident ray emanating from the image viewed, whose size is to be determined. Such being the case, the ray  $ac$ , according to the law of refraction, will be bent ( $ci$ ) toward the perpendicular  $nk$ , as it passes through the glass and away from the perpendicular, as  $il$ , and parallel with  $ac$  as it emerges from the glass, and the angle  $acn$  will be equal to the angle  $lim$ , parallel rays falling upon parallel sur-



faces. Now since the angle of incidence  $acn$  or  $a$  bears such a relation to the angle of refraction  $ick$  or  $B$ , that  $\frac{\sin a}{\sin B} = \text{index of refraction} = 1.65$  in case of flint-glass, it follows that  $\sin a = 1.6 (\sin B)$ , or,  $\sin B = \frac{\sin a}{1.6}$ —that is, when we learn the value of  $a$  by observation, we can find the value of  $B$  by trigonometric tables. The relation of the angle of incidence being to that of refraction, such as just described, the point  $a$ , to the eye of an observer at  $l$ , would appear to be at  $b$ , the glass plate effecting, therefore, a lateral displacement of the point  $a$ , to an extent  $ab$ , which is measured by determining the equal distances  $cf$ . The latter being equal to the hypotenuse into the sine of the opposite angle—that is,  $cf = ci \sin cif$ , it follows that if we can determine  $ci$  and  $\sin cif$ , we will obtain  $cf$  or its equal  $ab$ , the lateral displacement, or that which we desire to determine. Since the base  $kc$  is equal to the hypotenuse  $ci$  into the cosine of the adjacent angle  $ick$  or  $B$ —that is, that  $kc = ci \cos B$ , it follows that  $ci = \frac{KC}{\cos B}$ , and as  $kc$  is equal to the thickness of the glass

plates, which is known, we may call it  $T$  and say that  $ci = \frac{\cos B}{T}$ .

Further, the angle  $cif$  is equal to the angle  $hif$ , less the angle  $hic$ , but  $hif$  is equal to the angle of incidence  $nea$  or  $a$ , in that their sides are parallel, and the angle  $hic$  is equal to the angle of refraction  $ick$  or  $B$ , in that they are alternate angles, therefore  $cif = hif - hic$ , or  $\sin cif = \sin (a - B)$ . Substituting these values of  $ci$  and  $\sin cif$  in the formula  $kc = ci \sin cif$ , we obtain  $kc$  or  $ab = T \sin \frac{(a - B)}{\cos B}$ . Inasmuch, however, as there are two plates in the ophthalmometer, the complete formula will be

$$ab \text{ or } L = \frac{2T \sin (a - B)}{\cos B},$$

that is to say, the lateral displacement will be equal to twice the thickness of the glass multiplied by the difference between the sine of the angle of incidence and the angle of refraction divided by the cosine of the latter. Suppose, for example, that the thickness of the glass plate be 0.325 mm. the index of refraction of the flint glass plate 1.65, the angle of incidence or  $a = 6^\circ$ , as observed by the ophthalmometer, the angle of refraction  $B = 3^\circ 48'$ , as learned from the value of the angle  $a$  by trigonometric tables, then the lateral displacement will be

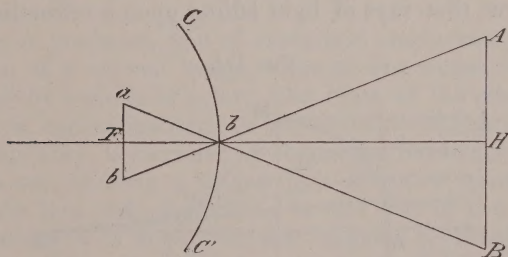
$$L = 2 \times 0.325 \frac{\sin (6^\circ - 3^\circ 48')}{\cos 3^\circ 48'}$$

and using logarithms  $L = 0.025$  mm.

In using the ophthalmometer the instrument should be placed in the dark chamber that is in a room with blackened walls, from which all sunlight can be excluded, and at a distance of ten feet from the eye

under examination, and on a level with it. A lighted candle being placed on the right- or left-hand side of the eye to be examined, on the left side for the left eye, on the right side for the right eye, as near as possible, and a screen intervening to protect the eye from the glare, by means of three small rectangular mirrors fixed by universal joints to a graduated wooden rod the light from the candle is reflected upon the eye. The vernier of each scale of the ophthalmometer further being at zero, and the instrument focussed, the observer on looking through the telescope at the eye under observation, will then see three minute specks of light upon the cornea, thus,  $\triangle \triangle \triangle$ . If now, however, the rotating screws be turned, which has the effect of placing the plates of glass obliquely, six minute specks of light will be seen on the cornea, thus,  $\triangle_a \triangle_b \triangle_c \triangle_d \triangle_e \triangle_f$ ,  $abc$  representing one-half of the amount of displacement in the one direction,  $def$ , one-half the amount in the other direction—that is to say, the three original images have been displaced through a distance equal to that between the two extreme images. Observing now the angle through which the plates have been moved, of the angle of incidence  $= a$ , and substituting the same in the formula just developed, the size of the corneal image due to the reflection of the light of the candle from the three mirrors will be determined. In using the ophthalmometer, it is not absolutely necessary to make use of the three mirrors just described, since as originally used, the object thrown upon the cornea was the distance between three candle flames placed beside the experimenter, two on his right hand, and one on his left. In order to avoid any calculations, Donders' suggests that a scale be prepared, in which each degree or fraction of a degree corresponds to a certain size in millimetres, the size of the corneal image being then determined by simply referring to the scale. It will be

FIG. 473.



To illustrate relation of size of object, to size of virtual image.

remembered that the object of determining the corneal image, as well as that of the image of the lens, also accomplished by the ophthalmometer, though in a slightly modified manner, was to determine the radius of curvature of the cornea, etc. Now from an inspection of Fig. 473, it is evident that the size of the object  $AB$  is to that of its virtual image  $ab$ —(that is, the image formed through the prolongation of the

<sup>1</sup> Accommodation and Refraction of the Eye, trans. by Moore, p. 19. London, 1864.



rays), as the distance  $HG$  of the object from the cornea  $CC'$ , is to the distance  $FG$ , or half the radius  $R$ —that is,  $AB : ab :: HG : \frac{1}{2}R$   
or

$$\frac{1}{2}R = \frac{ab \times HG}{AB} \text{ or } R = \frac{2(ab \times HG)}{AB}.$$

Let us suppose that the size of the corneal image  $ab$  has been determined by the ophthalmometer to be equal to 1 mm., to obtain  $R$  it only remains, then, to determine the value of  $HG$  and  $AB$ . This is done directly by measuring the distance between the upper and lower reflecting mirrors, which gives the size of the object  $AB$ , and measuring the distance from the cornea to the centre of the rod holding the mirrors and doubling the distance, since the light passes from the eye to the mirror, and thence back to the eye again, which gives the distance of the object from the cornea. Suppose that the size of the object  $AB$  should be 1000 mm., and the distance  $HG$  3800 mm., then

$$R = \frac{2(1 \times 3800)}{1000} \text{ mm.} = 7.6 \text{ mm.}$$

—that is, the radius of curvature in such an eye would be 7.6 mm., which differs but little from the radius of curvature of the short-sighted, or myopic eye, when at rest.

The index of refraction of the aqueous and vitreous humors, of the crystalline lens, the radius of curvature of the cornea and crystalline lens being determined in the manner just described, we are enabled, by means of formulæ, as already mentioned, to fix then the six cardinal points, by means of which, as has been shown, the paths of the rays of light through the media of the eye can be constructed, and the position and size of the image of the external object can be determined. While it is true that rays of light falling upon a refracting surface are

FIG. 474.

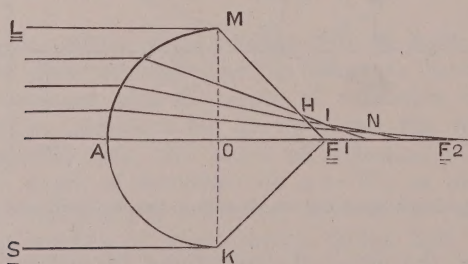
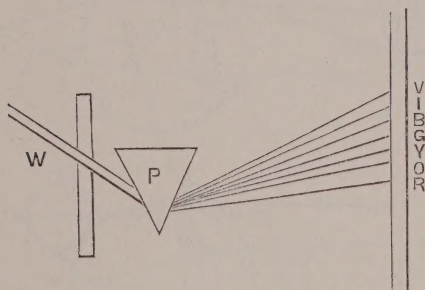


Diagram illustrating aberration of sphericity. (McKENDRICK.)

brought to a focus in essentially the manner we have described in treating of such surfaces, it must be mentioned in this connection that of rays impinging upon a refractive surface, the peripheral ones being more refracted than the central ones are not brought to exactly the same focus as that of the latter, there being, in fact, many foci, and the

image of the object consequently blurred and ill-defined. This condition, known as the aberration of sphericity (Fig. 474), and corrected in the making of lenses for microscopes, etc., by appropriate means, obtains also in the eye, though not to any marked extent, on account of the following circumstances: 1st, that the lateral most refracted rays are cut off by the iris, the latter acting precisely like the diaphragm of optical instruments; 2d, that the curvature of the cornea being ellipsoidal the lateral rays are less deviated than if the curvature was spherical; 3d, that the anterior and posterior surfaces of the crystalline lens are so disposed that the one corrects, to a certain extent, the action of the other; 4th, from the fact that the refractive power of the lens, diminishing from the centre to the circumference, the lateral rays are but little refracted. Inasmuch as a refracting medium does not act equally upon the different colored rays of which white light is composed, a ray of light in passing through a biconvex lens, for example, is not only bent, but decomposed into the colors of the spectrum (Fig. 475),

FIG. 475.



Decomposition of white light by prism.

the condition so produced, that of chromatic aberration, giving rise to the formation of a colored image, white at the centre, but surrounded at the borders by a circle of colors, like those of the rainbow. In the construction of optical instruments the chromatic aberration, or aberration of refrangibility, is corrected by combining lenses having a different dispersive power, as when a convex lens of crown glass is combined with a concave lens of flint glass, so, in the case of the eye, the chromatic aberration is, to a considerable extent, corrected through the crystalline lens, being composed of various layers of different consistence, and of different refractive power. As a general rule, indeed, we are unaware that our eyes are not achromatic, like the lenses of microscopes and telescopes, but, under certain circumstances, our attention is very forcibly called to the fact. Thus, if, after looking at the cross hairs of an astronomical glass by a red light, we try to see them with another colored light, violet, for example, the eye must be changed, the eye, when adapted to see with a red light, not being able to see by the violet. Again, if we look at a candle-flame through cobalt blue glass, which transmits only the red and blue rays, the flame may appear blue surrounded by violet, or *vice versa*, according as the eye has been accom-



modated for different distances. It may be also mentioned that red surfaces always appear nearer than violet ones, since the eye, having to be accommodated more for the red than for the violet one, imagines the former surfaces to be nearer than the latter. In addition to the aberration of sphericity and of refrangibility, more or less present in the eye, from the fact of the focal length of the vertical meridian of the cornea being sharper than the horizontal median rays of light emanating from a point, do not converge to one. The condition so caused, and constituting astigmatism, is a defect from which few eyes, if any, are free. That the eyes are astigmatic one can readily convince himself by simply looking (Fig. 476) at two threads crossing each other at right

FIG. 476.

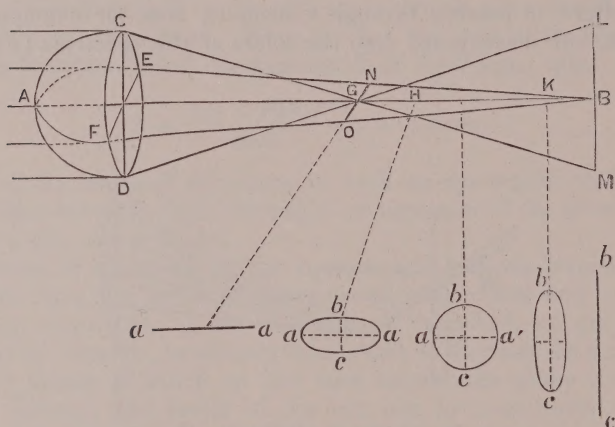


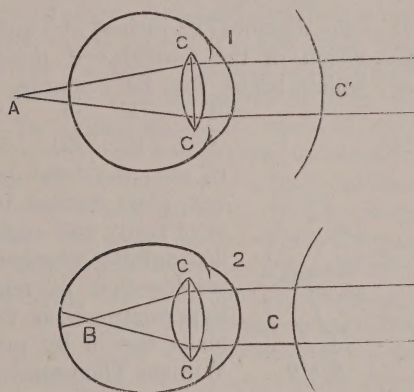
Diagram illustrating astigmatism. Lower figures illustrate appearance of rays, eye being at G H I, respectively. (McKENDRICK.)

angles in the same plane, or at two lines drawn in ink on a sheet of white paper disposed in a similar manner, when it will be observed at the point of distinct vision that it is impossible to see both threads, or lines with equal distinctness at the same time; that to see the horizontal line distinctly, for example, the paper must be brought near the eye, and removed from it, to see the vertical line.

While the detailed consideration of the subject of astigmatism belongs rather to the ophthalmologist than physiologist, it may be incidentally mentioned that the astigmatism of the cornea is, to a certain extent, naturally corrected by that of the lens, since the focal length of the vertical meridian differs from that of the horizontal, but in the reverse sense from that of the cornea. The actual degree of astigmatism present is measured by the difference in the refraction of the two chief meridians. Thus, if  $F^1$  = the greater focal length, and  $F^2$  = the smaller, then the astigmatism will be  $As = \frac{1}{F^1} - \frac{1}{F^2}$ , which can be corrected by the use of a cylindrical glass, the curvature of which is such that if added

to that of the horizontal meridian, will make its focal length equal to that of the vertical one. The defects of the eye due to aberration of sphericity and refrangibility, or astigmatism, are so slight, usually, as not to attract attention; near-sightedness and far-sightedness are, however, unfortunately so common, and interfere to such an extent with vision, as to necessitate the wearing of glasses. The cause of myopia and hypermetropia, and their treatment constituting, like astigmatism, one of the most important subjects of ophthalmology, do not demand in this connection special consideration. As still further illustrating, however, the manner in which the rays of light are brought to a focus in the eye, and serving in a measure also to elucidate the manner in which the eye is accommodated for different distances, a brief description of these abnormal conditions may not appear superfluous. Let us suppose, for example, that either through elongation of the whole eye or through the greater converging power of the lens (Fig. 477, 2) that rays of light

FIG. 477.



Hypermetropic eye and myopic eye (far-sighted and near-sighted eye). 1. Hypermetropic eye. The luminous rays arriving from an infinite distance (parallels) produce an ocular cone, the summit of which falls beyond the retina (at A), either because the cone is too long (lack of converging power in the media of the eye), or because the retina is too far forward (the eye being too short). 2. Myopic eye. The luminous rays from an infinite distance (parallels) produce an ocular cone, the summit of which falls in front of the retina (at B), either because this cone is too short (excess of converging power in the media), or because the retina is placed too far back (the eye being too long). Donders's researches seem to show that short-sightedness is owing to this latter cause, as is well shown in the figure (the ocular globe being greatly elongated from back to front). (KUSS.)

from an object are brought to a focus, not on the retina but in front of it, with the effect that two blurred indistinct images instead of one are seen. Obviously, in order to see distinctly under such circumstances, the object must be brought close to the eye so that the rays of light may be brought to a focus on the retina, hence the eye is said to be short-sighted or myopic. Evidently, however, if a concave lens (C) be placed between the myopic eye and the object, the rays of light will be made to diverge to such an extent that they will come to a focus on the retina, the formula made use of being as follows:  $\frac{1}{f} = \frac{1}{d} - \frac{1}{D}$ , in which



$f$  = the focal distance of the concave glass needed,  $d$  = the distance, 8 inches, say, at which the object is held for the short-sighted eye,  $D$  = the normal distance, usually taken as 10 inches, then  $\frac{1}{f} = \frac{1}{8} - \frac{1}{10}$

$= \frac{1}{40}$ —that is to say, 40 inches is the focal distance of the concave

glass needed. On the other hand, let Fig. 477, 1, represent an eye in which either the whole eye is too short or the lens not sufficiently convex; then the rays of light will come to a focus behind the retina, two blurred objects being seen. In order to see the object distinctly, the latter must be removed to a distance from the eye, hence the eye is said to be far-sighted or hypermetropic. Such being the case, obviously if a convex lens ( $C'$ ) be placed between the hypermetropic eye and the object, then the rays of light will be made to converge and come to a focus on the retina, the formula made use of to obtain the glass needed

being as follows:  $\frac{1}{f} = \frac{1}{D} - \frac{1}{d}$ , in which  $f$  = the focal distance of

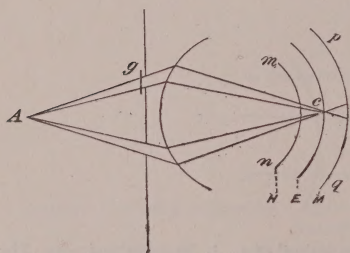
the convex glass,  $D$  = the distance (10 inches) at which the object would be held for distinct vision in the normal eye,  $d$  = the distance for the long-sighted eye which, let us say, for example, is 30 inches, then

$$\frac{1}{f} = \frac{1}{10} - \frac{1}{30} = \frac{2}{30} = \frac{1}{15}$$

—that is to say, the focal length of the convex glass needed is 15 inches.<sup>1</sup> A very ready and ingenious method for determining whether an eye is emmetropic—that is, normal, myopic, or hypermetropic, is that suggested and made use of by my colleague, Prof. William Thomson,<sup>2</sup> which consists in placing a piece of colored glass ( $g$ ), red, for example, over one of the openings in the card used in Scheiner's experiment, as represented in Fig. 478. Supposing the eye to be emmetropic, it is evident that the colored red ray and white ray falling upon the retina at the same spot, but one image, a red one, will be observed.

If the eye be myopic, however—that is, the retina is too far back, then through the crossing of the rays of light two images will be seen, a red one below and a white one above. On the other hand, if the eye be hypermetropic the images will be seen, but the red one will be above the white one below.

FIG. 478.



Scheiner's experiment, with Thomson's modification. A. Source of light. E. Position of retina in regard to the focus C of the rays entering through two apertures in a card, one of which is covered with a colored glass  $g$  in an emmetropic eye. H. Position of the retina  $mn$  in a hypermetropic eye. M. Position of retina  $p q$  in a myopic eye.

<sup>1</sup> In explaining to an audience the manner in which astigmatism, myopia, and hypermetropia, are produced the author has found the artificial eye of Kuhne, as made by Jung, of Heidelberg, a very useful adjunct.

<sup>2</sup> American Journal of the Medical Sciences, April, 1870.

## ACCOMMODATION.

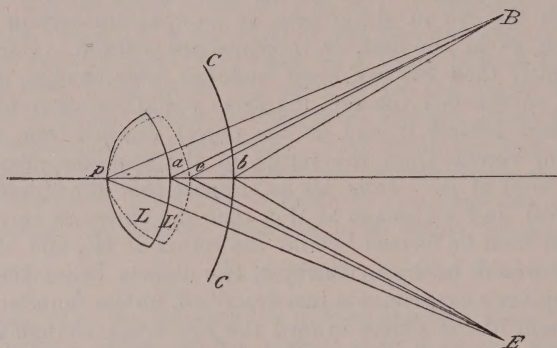
In considering the manner in which the rays of light are refracted as they pass through the media of the eye, and the image of an external object formed upon the retina, we have supposed heretofore that both the eye and the object were at rest. Every one is familiar with the fact, however, that, notwithstanding that an object may approach or recede from the eye in either case, at least within certain limits, it is clearly seen, as in the first, or intermediate position. Such being the case, evidently then the eye must undergo some change, otherwise, as the object approached the eye, the focus would recede from the retina, being formed behind it, and as the object receded from the eye the focus would recede from the retina in the opposite direction, being formed in front of it. Thus, let us suppose that the object being at A B (Fig. 469), and its image at d c, that the object is moved to H, its focus would then be formed behind the retina at H', and the condition of the eye would be hypermetropic, two objects being seen, as in the case of Scheiner's experiments just described, unless simultaneously with the movement of the object toward the eye some change was induced in the latter, by which the focus was kept upon the retina at d c. On the other hand, if the object be moved to M, then the focus would be formed in front of the retina, as at M', and the condition of the eye would be myopic, two objects being seen, unless simultaneously with the movement of the object from the eye, by some change in the latter, the focus was kept upon the retina at d c. The change undergone by the eye, and by which the image of the object is kept upon the retina, whether the object approaches or recedes from the eye, is known as the power of accommodation, and is without doubt due to a change in the shape of the lens; the latter becoming more convex as the object approaches the eye, less so as the object recedes from it; the lens becoming more convex as the object approaches the eye, the effect of the greater converging power of the lens, which would otherwise bring the focus forward toward M', is neutralized, so to speak, by the movement of the object toward the eye, which would otherwise remove the focus backward from the retina toward H, the focus, therefore, remains in the same position, d c. On the other hand, the lens elongating, becoming less convex as the object recedes from the eye, the effect of the greater diverging power of the lens, which would otherwise send the focus backward from the retina toward H, is neutralized by the receding of the object from the eye, the effect of which would otherwise be to draw forward the focus from the retina to M'; the focus, therefore, remains at the same place on the retina, d c.

Before considering the means by which this change in the shape of the lens is effected, and through which the eye accommodates itself to different distances, let us first show how it can be experimentally demonstrated that such a change in the shape of the lens, as that just described, does actually occur during accommodation. With that object let a person, whose eye is to be examined, be requested to look at some distant object, and while doing so let the light from the flame of a candle (B, Fig. 479) fall upon the eye (C C') at about the angle represented in



the figure; if the eye of the observer be situated at  $E$  three images will be seen; the first ( $a$ ) an erect virtual image, like that represented in Fig. 480, due to the reflection of the light from the cornea ( $b$ ) to the eye of the observer at  $E$ ; the second ( $b$ ) also a virtual erect image due to

FIG. 479.



Change in the form of the lens during accommodation.

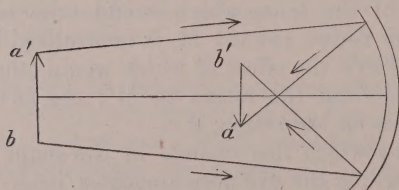
the reflection of the light from the anterior surface of the crystalline lens; the third ( $c$ ) a real reversed image, like that represented in Fig. 480. The three images being observed, let now the individual, whose

FIG. 480.



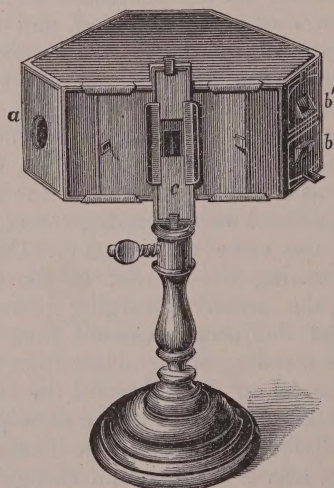
Reflected images in the eye. (DALTON.)

FIG. 481.



Real reversed image of concave mirror.

FIG. 482.



Phakoscope of Helmholtz. (McKENDRICK.)

eye is being examined, look at a near object, and at once the observer at  $E$  will notice that, while the position of the images (Fig. 480)  $a$  and  $c$ , due to the reflection of the light of the candle  $B$  from the cornea and posterior surface of the lens, remains unchanged, that of the image  $b$ ,

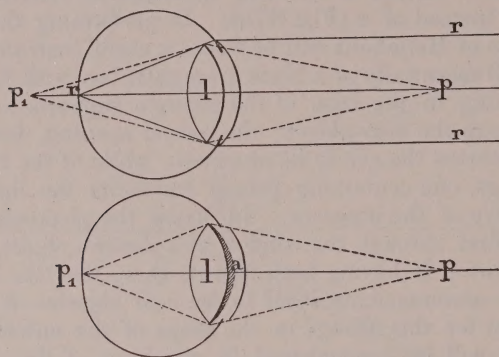
due to the reflection of the light from the anterior surface of the lens is very much changed, it being now much closer to  $a$ , and also that it is smaller than when the individual, whose eye is being observed, looked at a distant object, which can only be accounted for on the supposition that the anterior surface of the lens increases in convexity, the light falling upon  $l$  instead of  $a$  (Fig. 479). In performing this experiment the phakoscope of Helmholtz will be found a useful instrument. It consists (Fig. 482) essentially of a black triangular box with four openings: the first opening in the base of the triangle supports a needle point, which constitutes the near object; the second opening, directly opposite to the first, receives the eye to be observed; while of the two remaining lateral openings, one containing prisms transmits the light, the other receives the eye of the observer. In using the phakoscope the individual looks first through the window at a distant object, and then at the middle point. It having been shown, then, that the lens becomes more convex—accommodates itself to see near objects—it only remains now to account for this change in the shape of the anterior surface of the lens. It will be remembered, in speaking of the action of the ciliary muscle, it was mentioned that, owing to its disposition with reference to the sclerotic and choroid, that in contracting it would draw the choroid forward, thereby relaxing the suspensory ligament of the lens, the effect of which would be that the lens, owing to its elasticity, would change its shape.

It would appear, therefore, that the change in the convexity of the lens, through which the eye accommodates itself to see near objects, is brought about by the contraction of the ciliary muscle. If such be the case, of which there can be but little doubt, the sense of effort which we experience in looking at near objects must arise from the contraction of the ciliary muscle. Accommodation can only take place within a certain range, marked variation being observed however in this respect according to individual peculiarities. As a rule, objects situated at a distance from the eye of 6.5 metres (20 feet) or beyond to infinity, the punctum remotum or far point to be seen, do not necessitate accommodation, the parallel rays of light coming to a focus on the retina. The nearer however the object approaches within this limit, the eye, the more the accommodating power is exercised until a point is reached about 12 cm. (5 inches) from the eye, the punctum proximum or near point, which, if exceeded by the object, cannot be compensated by any further change in the shape of the lens. The accommodation being then strained to its uttermost if the object comes still nearer the eye, the rays of light will not be focussed upon the retina. The range of accommodation of the eye for distance lies then between these two limits, that of the punctum remotum and punctum proximum. The power of accommodation of the eye can be measured by the converging power of a lens, which gives distinct vision of an object placed at the punctum proximum without necessitating any accommodation in the eye—that is, of a lens which brings the diverging rays of light from the punctum proximum to a focus on the retina, just as if they had come parallel from the punctum remotum, for which accommodation is not required in the normal eye. Indeed, that is exactly the effect of the change in the



shape of the crystalline lens in accommodation, viz., that of retaining on the retina the focus of the rays of light diverging from the near point just as if they came parallel from the far point. The focal length

FIG. 483.

Condition of refraction in the normal *passive* eye during accommodation.

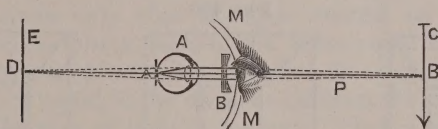
of such a lens is obtained from the formula  $\frac{1}{f} = \frac{1}{P} - \frac{1}{R}$  (1), in which  $f$  = the focal length of the lens,  $P$  = the distance of the punctum proximum (12 cm. = 4.8 inches),  $R$  = that of the punctum remotum, which in the normal eye equals infinity, therefore  $\frac{1}{f} = \frac{1}{12}$  cm., that is

to say, 12 cm. is the focal distance of the convex lens, representing the power of accommodation. As the elasticity of the lens diminishes as a result of age and as further it becomes more flattened, the lens gradually loses the power of changing its shape, of becoming more convex as an object approaches the eye, and consequently the punctum proximum recedes further and further from the latter. The diminution in the range of accommodation so produced is known as presbyopia, which, it will be observed, is an anomaly of accommodation, differing therefore from myopia and hypermetropia, which are anomalies of refraction. While the treatment of presbyopia belongs rather to the ophthalmologist than to the physiologist, it may be mentioned that it can be corrected by placing a lens before the eye, such as would give the rays the direction they would have if they came from the normal punctum proximum—the focal length of the lens required being obtained from the formula  $\frac{1}{f} = \frac{1}{P} - \frac{1}{p}$ , in which  $f$  = the focal length,  $P$  = the normal punctum proximum, and  $p$  = the punctum proximum of the presbyopic eye. Suppose the latter to be 30 cm. (12 inches), then  $\frac{1}{f} = \frac{1}{12} - \frac{1}{30} = \frac{1}{20}$ , that is, the lens required must have a focal length of 20 cm. (8 inches). In concluding the subject of refraction and accommodation, it may not appear superfluous if a brief account of the ophthalmoscope invented by Helmholtz be offered, by which the fundus of the

normal and diseased eye is examined, and through which, in the hands of Donders, Graefe, and others, ophthalmic medicine was revolutionized.

The interior of the eye under ordinary circumstances appears dark, since the observer being between the eye to be observed and the source of light intercepts the very rays whose reflection from the interior of the eye would form the image that it is desired to see. Further, the diverging rays from the interior of the eye converging as they pass through its media, are brought to a conjugate focus outside of the eye, which, to be seen, would have to be viewed by the observing eye at a distance equal to that of distinct vision—that is, so far from the observed eye, that little or nothing could be distinguished. If, however, the interior of the eye be illuminated by light reflected from a concave mirror the centre of which is perforated, and through and behind which the observer can view the eye, then the conjugate focus formed as just described by the rays reflected from the interior of the eye, can be more or less distinctly seen. The image of the retina, entrance of the optic nerve, etc., as viewed by such a mirror as that just described, and constituting the original ophthalmoscope, become, however, much more distinct, if in addition to the mirror the observed eye be viewed through a lens. Suppose that the lens used be a concave one, then rays of light emanating from a point of the retina (A, Fig. 484) (the illuminating

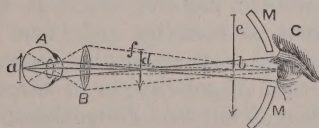
FIG. 484.



The ophthalmoscope with erect image.

rays from the mirror (M) being omitted in the figure for simplicity), which would be brought to a focus at B, the image being then real, magnified, and inverted by the action of the interposed diverging lens, whose focal distance is  $PB$ , are brought to a focus at D, the image being virtual, magnified but erect; that is, the rays which come to the observer's eye from the retina (A) appear through the action of the lens to come from D. On the other hand, suppose that the lens used be a convex one, then (Fig. 485), the rays from the retina (A) which would

FIG. 485.



The ophthalmoscope with inverted image.

otherwise come to a focus at B through the still greater converging effect of the lens, will come to a focus at  $d$ , the image formed being real and inverted, and, while larger than its object ( $a$ ) on the retina, is smaller than the image formed when the concave lens is used.

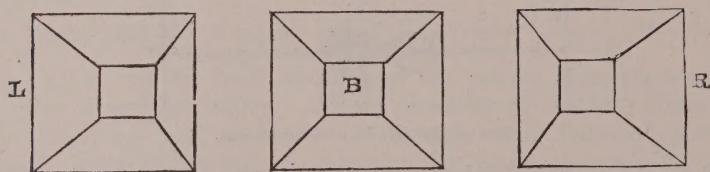


## CHAPTER L.

### BINOCULAR VISION. SENSATION AND PERCEPTION OF SIGHT. PROTECTIVE APPENDAGES OF THE EYE.

IN describing the manner in which vision is effected we have hitherto supposed it as being accomplished by a single eye; it remains for us now to consider how both eyes act in viewing objects, or binocular vision. It might be naturally supposed from seeing an object single, when viewed with one eye, that it would appear double when viewed with both eyes. A little observation will, however, make it clear that with one eye we see but one side, so to speak, of an object, the right side, for example, with the right eye, the left side with the left eye, and that in order to obtain a perception of the entire object we must see the two sides of the object simultaneously. Thus, for example, when we look at a truncated pyramid (Fig. 486, B) placed in the

FIG. 486.



Illustrating the principle of the stereoscope and binocular vision.

middle line before us, the image falling upon the right eye is such as represented at R, that upon the left eye at L, the perception of the form of B is the projection, being only obtained when the object is viewed by both eyes simultaneously. When two dissimilar images, one of the one eye, and the other of the other, thus fused into one perception, the inference by the mind is that the object giving rise to the images is solid. Such, indeed, is the principle of the stereoscope, in which two slightly dissimilar pictures, such as would correspond to the images of two objects as seen by each eye respectively, are by means of mirrors or prisms cast upon the retina so as to give rise to a single perception, that of solidity, or of three dimensions, though each picture has a surface of but two dimensions. In order, however, that the two retinal images shall be fused into the one mental perception, it is essential that the two images shall fall on corresponding points of the retina, at  $aa'$ ,  $bb'$ ,  $cc'$  (Fig. 487), otherwise there will be double vision—hence, in viewing an object with both eyes the latter are converged, the angle made by the axes of the two eyes being large if the object is near, and small if the latter be distant. It

will be observed further, from an inspection of Fig. 487, that since  $ab = a'b'$ , that the angle  $1 = 1$  and the angle  $1' = 1'$ , and that since the angle  $2 = 2$  the angle  $3 = 3$ , and that since  $bc = b'e'$ , that the angle  $4 = 4$ ,  $5 = 3$ . But it follows from the angles  $33$  and  $5$  being

FIG. 487.

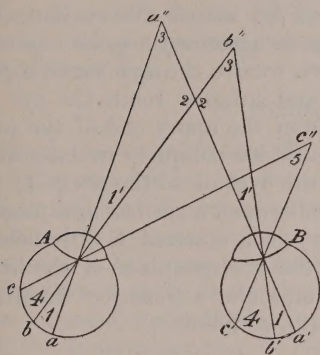


Diagram to illustrate theory of corresponding retinal point. (McKENDRICK.)

FIG. 488.

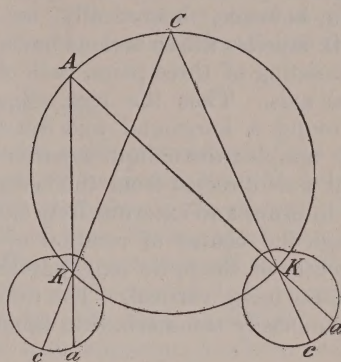


Diagram to illustrate the horopter. (McKENDRICK.)

equal, that  $a''$ ,  $b''$ ,  $c''$ , cannot lie in a straight line, it being the property of a circle only that triangles erected on the same chord and reaching the periphery, have at the latter equal angles. The line joining the points  $a''b''c''$  must therefore be a circle<sup>1</sup> (Fig. 488), of which the chord is equal to the distance between the points of decussation ( $KK$ ) of the rays of light in the eye. Such a circle is known as the horopter, and all objects not lying in it are seen double, their images falling upon corresponding points of the retina. Standing upright and looking at the distant horizon, the horopter would be approximately for normal long-sighted persons, a plane drawn through the feet—that is to say, the ground on which they stand.

The eyeball nearly filling the cavity of the orbit, and resting posteriorly upon a bed or cushion of adipose tissue, is moved by six muscles, the *recti* superior and inferior, externus and internus, and the obliqui superior and inferior. The effect of these muscles when acting separately is quite apparent from their origin and insertion. The four recti in the order named, arising from the apex of the orbit around the margin of the optic foramen, pass straight forward, piercing the capsule of Tenon or the fibrous membrane surrounding the sclerotic, to be inserted into the latter tunic at about the third or fourth of an inch behind the margin of the cornea, move the eye upward, downward, outward, and inward. The superior oblique muscle, arising from the optic foramen, proceeds toward the internal angle of the orbit and terminates in a round tendon, which, passing through a fibro-cartilaginous ring or pulley, is thence reflected backward and outward to be inserted into the sclerotic between the superior and external recti muscles. Its

<sup>1</sup> Muller : Physiology, trans. by Baly, vol. ii. p. 1177. London, 1842.



action is to rotate the eyeball downward and outward. The inferior oblique muscle arising from the orbital plate of the superior maxillary bone close to the external border of the lachrymal groove passes outward and backward between the inferior rectus and the floor of the orbit to be inserted into the external and posterior part of the sclerotic. Its action is to rotate the eyeball upward and outward. It can be shown, however, theoretically, as well as by actual observation, that the six muscles whose actions have just been described may be regarded as consisting of three pairs, each of which rotates the eye round a particular axis. Thus the recti superior and inferior rotate the eye up and round a horizontal axis directed from the upper end of the nose to the temple; the obliqui superior and inferior obliquely round a horizontal axis directed from the centre of the eyeball to the occiput; the recti internus and externus from side to side round a vertical axis passing through the centre of rotation of the eyeball situated a little behind the centre of the optic axis, parallel to the median plane of the head, the latter being vertical. The different muscular actions just described may be briefly summarized in tabular form, as follows :

TABLE LXXXI.—ACTION OF OCULAR MUSCLES.

| Number of muscles acting. | Direction.            | Muscles acting.     |
|---------------------------|-----------------------|---------------------|
| One . . .                 | Inward,               | { Internal rectus.  |
|                           | Outward,              | { External rectus.  |
|                           | Upward,               | { Superior rectus.  |
| Two . . .                 |                       | { Inferior oblique. |
|                           |                       | { Inferior rectus.  |
|                           | Downward,             | { Superior oblique. |
|                           |                       | { Internal rectus.  |
|                           | Inward and upward,    | { Superior rectus.  |
|                           |                       | { Inferior oblique. |
|                           |                       | { Internal rectus.  |
|                           | Inward and downward,  | { Inferior rectus.  |
|                           |                       | { Superior oblique. |
| Three . . .               |                       | { External rectus.  |
|                           | Outward and upward,   | { Superior rectus.  |
|                           |                       | { Inferior oblique. |
|                           |                       | { External rectus.  |
|                           | Outward and downward, | { Inferior rectus.  |
|                           |                       | { Superior oblique. |

It will be observed, from what has just been said of the action of the ocular muscles, and as seen from a glance at Table LXXXI., that even in viewing an object with a single eye, that a considerable amount of muscular coördination must take place, since when the eye is moved in any other than the vertical or horizontal meridian three muscles at least must be stimulated, relatively to the amount of inclination of the visual axis needed. Such being the case in single vision, necessarily, then, the amount of muscular coördination required in binocular vision must be much greater. If the eyes of any person be observed, it will be noticed that the two eyes move alike, when the right eye moves to the right so does the left, and to the same extent if the object looked at be distant, if the right eye looks up so does the left, and so in every other direction. Briefly, then, the eyes move in such a manner that the

images of an object always fall upon corresponding points of the retina, the essential condition, as we have seen, for the production of single vision, the movements of the two eyes ceasing to agree with each other only when the power of coördination is lost, through disease or by alcoholic or other poisoning. By movements of the eyes apart, however, from those of the head, the extent of the field of vision may amount to as much as 200 in the horizontal and 200 in the vertical meridian, that of a single eye being about 145 for the horizontal and 100 for the vertical meridian.

#### SENSATION OF SIGHT.

Regarding the sensation of sight as due to the stimulation of the retina by light, observation teaches, as might be supposed, that the intensity and duration of the sensation will vary according to the strength of the luminous vibrations, and the length of time during which the latter continue to fall upon the retina. That the intensity of the sensation varies with that of the luminous object is a matter of daily experience, a wax candle, for example, appearing brighter than a rushlight. With a little experimentation it becomes soon apparent, however, that the ration of the sensation to the stimulus is not a simple one, since while the sensations increase as the luminosity of the object increases, the sensations increase less and less, until finally there is no appreciable increase of sensation however much the luminosity may be increased—that is to say, when a light reaches a given brightness it appears so bright to us that we cannot tell when it becomes any brighter. It is much easier, therefore, to distinguish the difference between two feeble lights than the same difference between two bright lights—in fact, if the latter be very bright it becomes then impossible. Thus, for example, while there is no difficulty in distinguishing between the light of a candle and that of a rushlight, it would be impossible to distinguish such a difference between the light of two suns, supposing the light of the one to be in excess of that of the other in the same ratio as that of the candle over that of the rushlight, just as an addition of half an ounce to twenty pounds will not be appreciated by the sense of weight. Further, it will be found that if we let the shadows of two rushlights, for example, fall upon white paper and then move one of the lights away until the shadow ceases to be visible, that in performing the same experiment with two wax candles the candle will have to be moved through the same distance as that of the rushlight before its shadow ceases to be seen, the smallest difference in light in both cases appreciable being invariably about the  $\frac{1}{100}$ th of the total luminosity made use of. In this connection it may be appropriately mentioned as elsewhere, that whether the sensation be that of sight due to the stimulus of light or of hearing, due to sound or of temperature, due to heat or of touch, due to muscular effort or to weight, that the smallest difference of appreciable sensation is invariably a constant fractional portion of the total force, the cause of the sensation made use of, differing, however, for the various sensations. Thus, for example, suppose that the eyes being bandaged and the hand extended and supported, successive weights, as a drachm, ounce, and pound be placed upon it, it will be found, whatever be the weight origin-

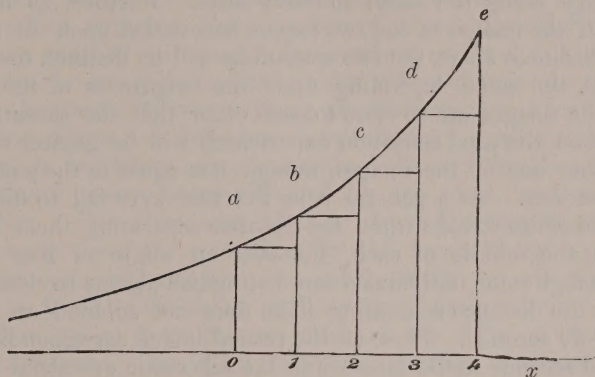


ally placed upon the hand, that in order to appreciate a distinct difference, one-third of the weight will be required to be added or taken away. In the case of muscular effort, however, only the  $\frac{6}{100}$ th of the original weight would have to be added or subtracted to make an appreciable difference in the sensation; thus a weight of 6 grains, added to 100 grains, would make a perceptible difference. In both the case of the sense of temperature or of sound the difference required, however, is the same as that of weight—that is to say, a difference of one-third of the total heat or sound giving rise to the initial sensation, added or subtracted, would be appreciated. It might naturally be supposed that vibrations such as those of light and sound, etc., in acting upon the terminal fibres of the optic and acoustic nerves, etc., might impress the latter so slightly as to give rise to no sensation whatever, and that if the strength of the stimulus be gradually increased, a very feeble excitation would be experienced, which might be called the lower limit or minimum of excitation. Such, indeed, has been shown experimentally to be the case, the minimum of excitation being in the case of the sensation of touch a pressure of 0.002 gramme to 0.03 gramme, in that of temperature  $\frac{1}{3}$  of a degree Cent., the skin being at a temperature of about  $18.4^{\circ}$  C., in that of muscular effort shortening to the extent of 0.044 mm. of the internal rectus of the eye, in that of sound a ball of pith 1 milligramme in weight falling through 1 mm. upon a glass plate, heard at a distance of 91 mm. from the ear, in that of light an intensity of about 300 times less bright than that of the full moon.

From what has been said with reference to sensory impressions it appears to have been well established: 1st, that there is a minimum of excitation—that is, the smallest possible excitation capable of producing a sensation; 2d, a maximum of excitation, over and above which no increase in the stimulus will give rise to any further increase in the sensation; 3d, that there is a constant proportion or ratio between the intensity of the excitant and the intensity of the sensation; 4th, that the intensity of the sensation does not increase proportionally to that of the stimulus or excitation. It is evident, therefore, that we have the means of measuring indirectly sensations, however impossible that might appear to be at first sight, since the excitation of any nerve giving rise to the sensation, being due to an external stimulus, can be, through the latter, arbitrarily varied, and therefore quantitatively determined. Further, the experimental determination of the constant proportional, and the minimum excitation, furnishes the data by which the law expressing the general relation of sensation to excitation can be graphically investigated and established. Suppose, for example, that the sensation under consideration be one of pressure, let the horizontal line  $ox$ , or the abscissa (Fig. 489), be divided into equal parts, 1, 2, 3, 4, to represent increments of sensation, the zero corresponding to the minimum of sensation, the vertical lines, or the ordinate  $0a$ ,  $1b$ ,  $2c$ ,  $3d$ ,  $4e$ , the increments of stimulus,  $0a$  corresponding to the minimum stimulus, say one-fiftieth of a gramme, each ordinate being equal to the preceding one plus a third of the same, according to the determination of the constant proportional in the case of weight; it is evident that the difference of length between the line  $0a$  and the lines  $1b$ ,  $2c$ ,  $3d$ ,  $4e$ ,

indicates the weights that must be used, in order that the perceptible difference in sensation should be doubled, tripled, quadrupled, quintupled; and which, if the sensations be as 1, 2, 3, 4, the weights, or their representation, the ordinates will be found to be as 10, 100, 1000, 10,000—that is to say, the sensation varies, not as the stimulus, but as the

FIG. 489.



Graphic illustration that sensation is proportional to logarithm of stimulus.

logarithm<sup>1</sup> of the stimulus, the numbers 1, 2, 3, 4, being the logarithms, respectively, of 10, 100, 1000, 10,000. To those familiar with the language of the calculus the above law, that of the sensation varying with the logarithm of the stimulus, or the Weber-Fechner law of sensation, may be briefly described as follows: Let  $s$ , a sensation, be a function of a stimulus  $x$ , then  $ds = K \frac{dx}{x}$  (1),  $ds$  being the smallest appreciable increment of sensation due to  $dx$ , the corresponding increment of the stimulus  $x$ , and  $K$  a constant. Integrating (1) we obtain  $s = K \log. x + c$ , which becomes  $0 = K \log. x' + c$  if  $x$  be diminished to  $x'$ , at which the sensation ceases—that is,  $c = -K \log. x'$ , and  $s = K \log. x - K \log. x'$ , or  $s = K \log. \frac{x}{x'}$ .

Returning from this little necessary digression to the sensation of sight, it is evident that the duration of the sensation is longer than that of the stimulus, the sensation of sight and the stimulus of light being comparable, in this respect, to a muscular contraction, as induced by a single induction shock. It is for this reason that if two flashes of light follow each other sufficiently quickly within the one-tenth of a second for a faint light, and the one-thirtieth of a second for a strong one, the two sensations arising are fused into one. Hence, the fact of a luminous point moving rapidly around in a circle giving rise to the sensation of a continuous circle of light, which reminds one of the production of muscular tetanus. That the duration of the stimulus of light necessary to give rise to the sensation of sight must be very short, is shown from the fact of the electric spark being seen, though the latter is known to

<sup>1</sup> A logarithm of a number is the exponent of the power to which it is necessary to raise a fixed number to produce the given number. Suppose the fixed number to be 10, the given number 100 or 1000, then 2 and 3 will be the logarithms of 100 and 1000 respectively, since  $10^2 = 100$ ,  $10^3 = 1000$ .



last but the  $\frac{1}{2500000}$ th of a second. When a large portion of the retina is affected by light the total sensation experienced is greater in amount than when a small portion is so affected, a large piece of white paper, for example, affecting our consciousness more than a small piece. If, however, the surfaces of the papers be equally and uniformly illuminated, the small piece will appear as bright, or white, as the large one, the intensity being the same in both cases. Further, as might be expected, if the images of the two papers be situated upon the retina at sufficient distances apart, the two sensations will be distinct, the relative intensity of the same depending upon the brightness of the objects, while, if the images are so close to each other that the sensation fuses into one, then the total sensation experienced will be greater than that due to either one of the images, though not equal to the sum of the single sensations. As a general rule, the best eyes fail to distinguish two parallel white streaks when the distance separating them, as measured from the middle of each, subtends an angle of less than 73 seconds, though some individuals can distinguish objects so close to each other that the distance separating them does not subtend an angle of more than 50 seconds. Now, as the retinal image corresponding to an angle of 73 seconds would measure in the schematic eye about the 5.36 of a micromillimetre (the  $\frac{1}{25000}$ th of an inch), and that corresponding to an angle of 50 seconds, about the 3.65 of a micromillimetre, and as the average diameter of a retinal cone measures at its widest part about 3 micromillimetres, it is evident that the visual sensory area has a corresponding physical basis in the retinal anatomical area, which renders it highly probable that there is still another corresponding cerebral or perceptive area.

It has already been mentioned that, owing to the unequal refrangibility of different kinds of light, that white light in passing through a prism is not only refracted, but is decomposed into the seven kinds of light of which white light is composed, viz., violet, indigo, blue, green, yellow, orange, and red, or the colors of the spectrum. In considering, however, the manner in which we become conscious of the different colors of which the spectrum is composed, or of any colors or color, we must disabuse ourselves at once of the idea that what we call color exists outside of our own consciousness objectively as such, since what we call color in ourselves subjectively, can be shown experimentally to be due objectively to a vibration, an oscillatory movement, a wave of a definite length passing into the eye at a certain velocity, all kinds of light being so propagated. In fact, color objectively is to the eye what we shall see pitch in the case of sound is to the ear, the latter depending solely upon the number of vibrations striking the ear in a second. In other words, a wave of a certain length, propagated at a definite rate, in falling upon the retina gives rise in us to a sensation of a particular color. Thus, the color red is due to the impinging upon the retina of a wave about the  $\frac{1}{39000}$  of an inch in length, travelling at such a velocity that about 474,439,680,000 such waves enter the eye in a second; the color violet to a wave about the  $\frac{1}{57500}$  of an inch, about 690,000,000,000,000 such waves entering the eye in a second, the waves giving rise to the violet color being shorter than those to which the red color is due, but following each other into

the eye more rapidly than the latter, the waves to which the other colors of the spectrum are due with reference to their length and velocity, lying between the extremes just mentioned. The sensation of color depending then upon the successive impulses imparted to the fibres of the optic nerve by waves of different length travelling at different velocities, it is obvious that it would be useless to look into the external world for any attribute or quality that would correspond objectively to what we call in ourselves the sensation of color. In other words, the color red or violet of an object is in ourselves, not in the object looking red, because the wave giving rise to red is reflected from the object into our eyes, the remaining waves being absorbed by the object; similarly surrounding objects look red when viewed through a red glass, the wave giving rise to red being alone transmitted through the glass to our eye the remaining waves being absorbed by the glass, and so with all other colors. Our knowledge of color depending then upon the impression made upon the sensorium by the waves of light, can never be absolute, but only relative. In other words we can never know the light in itself by the thing itself, or the "ding an sich" as Kant<sup>1</sup> expressed it, but only by just so much as the light or thing affects our consciousness. The extent to which sensation is dependent upon the susceptibility of the organism of being impressed by the external world, is shown by the fact, that notwithstanding the solar spectrum extends beyond the violet in one direction, and beyond the red in another, the eye under ordinary circumstances is unconscious of the existence of these extremes, being so organized as not to be affected by the ultra violet or chemical rays, or the ultra red or heat rays. Our knowledge being due to sensations arising from impressions made by the environment upon the organism, cannot then be innate, but must have been ultimately derived from experience, and therefore relative as held by Locke.<sup>2</sup> After what has just been said, it is evident that no physical or chemical changes in the retina will account for our sensation of color, since the cause of the latter lies not in the retina, which is simply an intermediate organ, correlating the physical with the psychical, but in that part of the cerebrum where the still physical vibration gives rise to sensation. Indeed, the cause of the sensation of color, as might be premised from the present imperfect state of physiological psychology, is not yet understood, although a great number of interesting observations have been made with reference to the effect of fusing colors of complementary colors, of which a brief account at least in this connection must be given.

Though we have spoken of the solar spectrum consisting of seven colors, as a matter of fact, it is made up not only of such, but also of a great number of intermediate tints as well. External nature presents the same tints, and also a number of others like those of purple, brown, gray, etc., which however, are not present in any part of the spectrum. While such tints are apparently due to distinct simple sensations, it can be shown experimentally that in reality they are compound ones, being obtainable by the fusion of two or more color sensations. Thus, purple

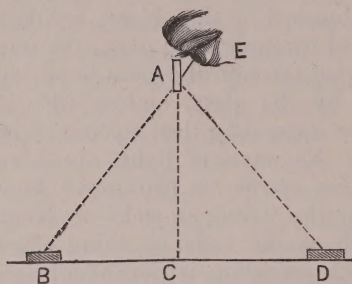
<sup>1</sup> Critique of Pure Reason, trans. by Max Muller. Second Part, p. 39. London, 1881.

<sup>2</sup> Of Human Understanding, Locke's Works, chap. ii. vol. i. London, 1883.



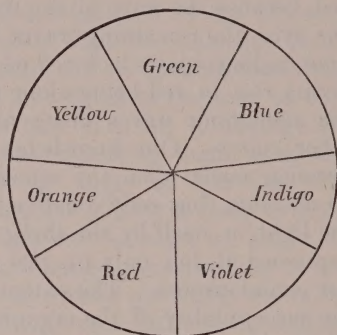
which, as just mentioned, is not present in the spectrum, may be readily produced by the fusion of red and blue, as, for example, by so placing a red and blue wafer and a glass (Fig. 490) that the light will be reflected from the red wafer (D) in the same direction as that coming from the blue wafer (B). In the same way the various tints of nature may be obtained by fusing different colors, sensations with that of white or black, different kinds of brown resulting from mixtures of yellow, red, white,

FIG. 490.



Lambert's method of studying combinations of colors.

FIG. 491.



Rotating disk of Sir Isaac Newton for mixing colors.

and black, grays from white and black, as can be shown by making use of a rotating disk, on the surface of which colored sectors are painted, the resulting color being white for example, in that of the instance represented in Fig. 491. Experimenting in this way, it can be shown that the quality of a color depends on the wave length of its constituent waves and on the relative amount of colored and white light falling upon the retina in a given time, a color being saturated when unmixed with white light, as in the case of the colors of the spectrum.

As regards the fusion of colors, it is evident from what has been said of the subject of color, that in mixing red and yellow to produce an orange, for example, undistinguishable from the orange of the spectrum, that the sensation of orange cannot be due to the uniting of the red and yellow waves differing in length from each other to form an orange wave differing in length from either, but that it is the mixture of the sensation of red and yellow that gives rise to the sensation of orange. In other words, the mixture is psychical not physical. It is an interesting fact, that certain colors, when mixed together in pairs in certain definite proportions, give rise to the sensation of white, as, for example, red and blue-green, orange and blue, yellow and indigo-blue, green-yellow and violet; such colors are said to be complementary colors, since given the color of one of the pairs, say red, all that is necessary or complementary to produce white is the other color of the pair, or green. It can be also experimentally shown, by means of the rotating disk, that the mixture in proper proportions of any three distinct colors of the spectrum arbitrarily selected but sufficiently far apart, as, for example, red, green, and violet, will produce white, and that by the further addition of white the

sensations of all the other colors can be obtained. In order to avoid any misunderstanding as regards the production of the sensation of white, it should be mentioned that the mixture of red, green, and violet pigments, unless they are perfectly pure, will not produce white; a mixture of pigments being totally different from a mixture of sensations of colors, since the color produced by the mixing of pigments is due to the light which has escaped absorption by the same rather than the color due to a mixture of the colors. For example, the sensations of indigo and yellow, when mixed, give rise to the sensation of white, the sensation due to the mixing of indigo and yellow pigments is, however, green, the indigo absorbing the red of the yellow and the yellow absorbing the blue of the indigo, green only being left for both to reflect. Facts like those just mentioned with reference to the fusion of colors, their complementary relation, the composition of white light, etc., led the celebrated Young,<sup>1</sup> in the beginning of this century, and Helmholtz,<sup>2</sup> in recent times, to advocate the view that all of our sensations of color are compounds of three primary color sensations, red, green, and violet, and that waves of different lengths give rise to all three of these sensations according to their particular length—that is to say (Fig. 492), the

FIG. 492.

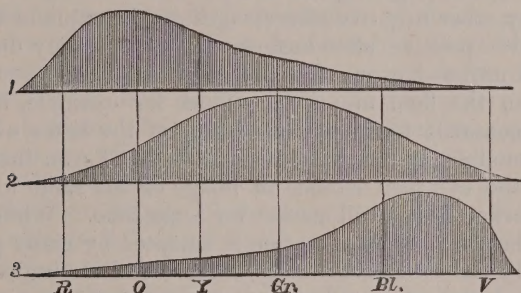


Diagram of three primary color sensations. 1 is the so-called "red," 2 "green," and 3 "violet" primary color sensation. R, O, Y, etc., represent the red, orange, yellow, etc., color of the spectrum, and the diagram shows, by the height of the curve in each case, to what extent the several primary color sensations are respectively excited by vibrations of different wave-lengths. (FOSTER.)

orange wave gives rise to much of the first sensation, or red, less of the second or green, and to little of the third or violet; on the other hand, that the blue wave gives rise to little of the red sensation, to more of the green, and to much of the violet, etc. The anatomical basis for the above is the assumption that three kinds of nerve fibres exist in the retina, the excitation of which gives rise respectively to the sensations of red, green, and violet—homogeneous light—all three of these so-called fundamental sensations, but with different intensities according to the length of the wave; long waves exciting most powerfully the fibres whose stimulation give rise to the sensation of red, medium waves those causing the sensation of green, short waves those causing the sensation of violet. Accepting provisionally the Young-Helmholtz theory of color sensation, it serves to explain some of the phenomena of color-blindness, after-images,

<sup>1</sup> Lectures on Natural Philosophy. London, 1807;

<sup>2</sup> Op. cit., p. 382.



etc. While almost all individuals are able to appreciate differences of color, there are some, and the number is far greater than usually supposed, who are unaffected by certain colors, the most common defect being an insensibility to red, blindness to green and violet being rare. Thus, for example, in Daltonism or blindness to red, so called on account of its having been observed in the celebrated Dalton, the red end of the spectrum appears dark, a red gown lying on a green grass plot, a red cherry among green leaves, are distinguished, not by their color but by their form, the color of the gown or the fruit appearing to such an eye not red but green like that of the grass or leaves. Remembering that green is the complementary color to red, and supposing that in a daltonic eye the fibres whose stimulation in an ordinary eye would give rise to the color of red, are either absent, diseased, or paralyzed, the phenomenon just referred to can be accounted for. Similarly if after a red patch has been looked at steadily for some time until the eye becomes fatigued, a white surface be looked at, a green patch will be seen instead of the red one, the green fibres of the retina, so to speak, being fresh, are susceptible of being excited by the green color (or wave giving rise to it) of the white light reflected from the paper, the red fibres being, however, exhausted, are no longer susceptible of being excited by the red color (or the wave giving rise to it) of the white light. In the same manner many other negative after-images can be explained, so called as contrasted with positive after-images which are simply due to a sensation, being continued even after the object giving rise to it has been removed from the field of vision. Thus, for example, if the eye be directed momentarily to the sun the image of the latter will be present for some time after, or if a window be looked at for an instant on early waking and the eye then closed, an image of the same with its bright panes and darker sashes will persist for some time. While the Young-Helmholtz theory of color sensation is accepted by many physiologists, another theory has been advanced by Aubert<sup>1</sup> and Hering<sup>2</sup> among others, the latter of whom maintain that the primary color sensations are white, black, red, yellow, green, and blue, and that these different sensations are due to the changes in the so-called visual substance of the visual apparatus, the changes giving rise to the sensations of black, green, and blue being processes of a constructive-assimilating kind, those giving rise to the sensations of white, red, and yellow, of a destructive-assimilating kind. If Hering's view be accepted, then black and white, green and red, blue and yellow, far from being complementary, must be regarded as antagonistic to each other, and the visual substance assumed to be always undergoing changes, never in a state of rest. The limits of this work will not permit of further illustration or discussion of the relative merits of the Helmholtz and Hering theories of the sensations of color; it may be pointed out, however, once more, that whether the one or the other theory be accepted, we are not a whit nearer the explanation of the sensation of color, since the transformation of the ultimate physical vibration or wave into the psychical color sensation takes place not in the retina but in the cerebrum.

<sup>1</sup> Physiologie der Netzhaut, 1866.

<sup>2</sup> Wien. Sitzbericht, lxvi. (1872), lviii., lxi., lxx.

## PERCEPTION OF SIGHT.

It has already been mentioned that as the apparent size of an object depends upon the visual angle, if two objects, though of different size, subtend with the eye equal angles—that is, if their visual angles are the same—the apparent size of the objects will be the same. The real size of an object is therefore not determined by the sense of sight, the latter only giving rise to the sensation of its apparent size. The estimate of the real size of an object is really an inference based upon its apparent size, but modified by the knowledge of its distance from the eye. In other words, it is not a simple sensation, but a judgment based upon the sensations of touch, as well as those of sight. Knowing the distance of an object from us, we infer from its apparent size its real size; and conversely, knowing the size of the object, we infer its distance. Thus if the image of some well-known object, a man, for example, appear in our field of vision, and we know how far off the man is, we infer his size from that of our retinal image; and, conversely, knowing the size of the man, if his retinal image be very small, we infer that the man is very far off. That our estimate of the size of an object is dependent upon the knowledge of its distance from us, is shown from the fact that if we have no means of even approximately estimating the latter, it is impossible to obtain any idea of its size. Thus the sun, though about four hundred times the distance of the moon, is apparently of the same size as the latter, but we infer from that very reason that the one body is larger than the other; did we not know, however, their relative distance from the earth, it would be impossible to say which of the two, the sun or the moon, was the larger body. Our estimate of the distance of objects is not only based upon their size, but largely upon the presence of surrounding and intermediate objects, it being difficult to estimate the distance of an object entirely isolated, as in looking at a single distant object at sea. The muscular sensations arising through the contraction of the ocular muscles in converging the visual axis for near objects, and diverging the same for distant ones, aid us very much in forming a correct judgment as to the distance of objects. As with our estimate of the distance of objects, so with that of the idea of solidity, which is essentially an estimate of the distance of the different parts of an object, the idea being a judgment, a mental combination of the two dissimilar pictures formed upon the retina, the image of the object as viewed by the right eye being, as already mentioned, different from that as viewed by the left eye, the resultant image being seen in relief, and giving rise to the idea of solidity. The fact that we see objects erect, though their images are reversed upon the retina, as already mentioned, is due to the fact of the sensation of the image derived from the sense of sight being modified by the sensation of the object derived from the sense of touch. The mind associating images situated at the upper and inner part of the retina with the objects giving rise to them but situated below and to the outer side of the eye, and images at the upper and outer part of the retina with objects situated below and to the inner side of the eye, and projecting outward, the images



or the luminous sensation back to the objects giving rise to them, finally perceives the objects erect. In the same way, but conversely, when a phosphene or luminous image is created by pressing, say on the outer or lower side of the eyeball, the image appears to lie above and to the inner side of the eye. Indeed, the association of the sense of sight with that of touch in obtaining the ideas of the size, distance, solidity, position of objects, etc., is so intimate, that were our knowledge of the same derived through the sense of sight alone, it would be of the most inexact and unreliable character. That such is the fact, has been shown by cases like those of the youth reported by Cheselden,<sup>1</sup> who for some time after the sense of sight was given him, he having been born blind, saw everything flat, as in a picture, and supposed that objects when seen, touched his eyes, as objects when felt, touched his fingers. The newly acquired sense of sight at first rather hindered him in finding his way about the house, which he could do perfectly well by the sense of touch alone. The fact that the youth could not tell of his two pets which was the cat, and which was the dog, by the sense of sight alone, though he could at once distinguish them by feeling them, led him one day to feel the cat and at once look at her, and then setting her down, said, "So puss, I shall know you, another time." What has just been said renders it very probable, as held by Locke,<sup>2</sup> that a person born blind, on suddenly obtaining his sight, would be unable by sight alone to distinguish a cube from a sphere—that is, to be able to say which was the sphere, which the cube, for though he knows how the sphere or the cube affects his touch, he has not learned by experience, as yet, that if the cube, etc., affects his touch so and so, it will affect his sight so and so, and enable him by sight alone to distinguish it from the sphere. Since our perception of external objects is elaborated out of the sensations that the retinal images give rise to, it might be supposed that the perception would invariably correspond to the sensation, just as the latter would correspond to the retinal image causing it. As a matter

FIG. 493.

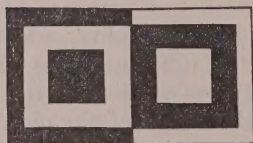
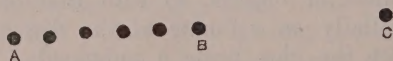


Illustration of irradiation. (McKENDRICK.)

FIG. 494.



Illusions of size.

of fact, however, such is not invariably the case, discrepancies arising between the retinal image and the perception, some of cerebral, others of retinal origin, the effect of which is so to modify the perception that the usually reliable judgment as to the size, distance, etc., of objects is perverted. Thus, for example, the white square (Fig. 493) on the black ground appears larger, and the black square on the white ground smaller, than it really is, the over-lapping of the white light in

<sup>1</sup> Phil. Trans., 1728, p. 477.

<sup>2</sup> Op. cit., Book II. chap. ix. p. 256.

either case, or the irradiation, being due, as it were, to retinal or cerebral fibres other than those directly stimulated by the light being thrown into sympathetic vibration. If a white strip be placed between two black ones, the inner edges of the former—that is, the edges nearest the black will appear by contrast whiter than the median portions. In the same manner, the centre of a white cross placed upon a black background, will often appear shaded, as compared with the remaining parts. The judgment may also be at fault with reference to size, as in Fig. 494, when though the distance *AB* is equal to the distance *BC*, the former appears to be the greater; or with reference to direction, as in the case of Zoellner's (Fig. 495) lines, which, if

FIG. 495.



Zoellner's figure, showing an illusion of direction. (McKENDRICK.)

looked at obliquely, will give the impression that the vertical lines, though parallel, converge or diverge, and the oblique lines, though continuous across them, are not exactly opposed to each other. That the above effect is due to an error of judgment, is shown by the fact that by an effort it may be controlled, the lines being then seen as they really are. If two equal squares be marked, one with vertical, and the other with horizontal, alternate dark and light bands, the former will appear broader, and the latter higher than it really is. Short persons should therefore wear dresses horizontally striped if they wish to increase their apparent height, and stout persons avoid wearing longitudinally striped ones. Many other such examples might be given, but the above will suffice to illustrate the errors of judgment that the sense of sight alone may lead one into.

#### PROTECTIVE APPENDAGES, ETC., OF THE EYE.

The eyeball, with its muscles, etc., is protected by the bony orbit, the outer wall of which is stronger than the inner one, the eye being



more exposed to injury from the outer than the inner side; the inner wall of the orbit projecting, however, considerably beyond the outer wall, the extent of vision is far greater in the outward than in the inner direction. The upper semi-circumference of the orbit and the superciliary ridge is provided with short, stiff hairs, the eyebrows, which serve to protect the eyelids from the perspiration of the forehead, and to shade the eye from excessive light. The eyelids consist of folds of very thin integument lined by mucous membrane, the conjunctiva, the subcutaneous connective tissue being thin, loose, and free from fat, and containing small papillæ, and sudoriferous glands. The eyelashes, the short, stiff curved hairs projecting from the borders of the lids in two or more rows, serve to protect the eye from dust, and, to a certain extent, also, to shade it. The palpebral cartilages, extending from the edges of the lids, which they support, to the margin of the orbit, are small, elongated, semilunar plates, attached internally by the *tendo-palpebrarum* to the lachrymal groove, externally by the external tarsal ligament to the malar bone, and supported by the palpebral ligament. On the posterior surface of the tarsal cartilages, lying just beneath the conjunctiva, are found the Meibomian glands, which, in structure, are modified sebaceous glands, whose secretion, an oily fluid, in smearing the edges of the eyelids, prevents the overflow of the tears. The eyelids serve to protect the eyeball, their movements constituting, respectively, the opening and closing of the eye, the act of winking favoring the passage of tears over the globe and through the lachrymal canals into the nasal sac; and hence, when the *orbicularis palpebrarum* is paralyzed, by the contraction of which muscle the eye is closed, the tears do not, as readily as usual, pass into the nose. The eye is principally opened by the raising of the upper eyelid through the contraction of the *levator palpebrarum*, though it is also opened through the elevation of the upper and depression of the lower eyelids, respectively, through the action of the plain muscular fibres existing in both eyelids, and which are innervated by the sympathetic, the *orbicularis palpebrarum* being supplied, as has already been mentioned, by the facial and the *levator palpebræ* by the third nerve.

The eyes are usually kept open, almost involuntarily, though we can close or open them at will; the action of the *orbicularis* muscle is, however, to such an extent of a reflex character, that if the globe of the eye be touched or irritated, or if the impression of light produces pain, it is then impossible to keep the eye open. It has already been mentioned that the inner surface of the upper and lower eyelids is lined by a mucous membrane, the conjunctiva. The conjunctiva, continuous with the membrane lining the *puncta lachrymalis*, and the lachrymal ducts, is reflected forward from the inner periphery of the lids over the eyeball, that lining the lids being called the palpebral, that covering the eyeball the ocular conjunctiva; the latter differing, further, in its sclerotic and corneal portions. At the point where the membrane is reflected upon the globe it presents a superior and inferior fold, the former containing numerous glandular follicles and minute lachrymal glands. At the inner canthus there is a vertical fold, the so-called *plica semilunaris*, which, morphologically, corresponds to the inner and third eyelid, or

the nictitating membrane present in many of the lower animals, as in sharks, birds, and some mammals. The canicula lachrymalis, the reddish spongy elevation situated at the inner portion of the plica just mentioned, consists of a collection of follicular glands with a few delicate hairs on its surface. The eye is kept continually moist by a thin, watery fluid secreted by the lachrymal gland, which, after being spread over the globe by the movement of the lids and of the eyeball, passes into the lachrymal apparatus, any overflow upon the cheek, constituting the tears, being prevented ordinarily by the secreting of the Meibomian glands. The lachrymal gland, about the size of an almond, ovoid in form, and of a racemose type of structure, is situated at the upper and outer portion of the orbit. It presents six to eight ducts, five or six of which open above, and two or three below the outer canthus of the eye. The tears consist largely of water, which amounts to over 90 per cent., the remaining elements being made up of small quantities of epithelium, albumen, sodium chloride, alkaline and earthy phosphates, mucus, and fat. The actual amount of the lachrymal secretion has not been determined. Every one is familiar with the fact that the secretion of tears is very much increased by emotion; hypersecretion may be also readily induced through reflex action by irritation of the conjunctiva, nasal mucous membrane, muscular effort, laughing, coughing, and sneezing, the efferent nerves involved being the lachrymal and orbital branches of the fifth nerve, branches of the cervical sympathetic; the afferent nerves varying according to the exciting cause. The lachrymal apparatus, through which the tears usually flow into the nose, begins by two little points or orifices, the puncta lachrymalis, which leads into the upper and lower lachrymal canals, the latter surrounding the canicula lachrymalis. Just beyond the canicula the canals unite and pass then into the lachrymal sac or the upper dilated portion of the nasal duct. The duct being about half an inch in length, fibrous in structure, and lined with ciliated epithelium, empties into the inferior meatus of the nose. Reflux of the tears from the nose to the eye is prevented by the folds of mucous membrane present in the lachrymal canals, and at the opening of the duct into the nose, acting as valves, the latter one acting, in this respect, much more effectually than the former.



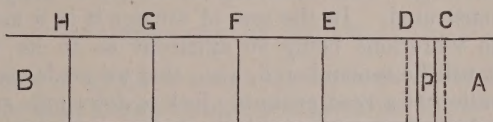
## CHAPTER LI.

### PHYSIOLOGICAL ACOUSTICS.

JUST as we have seen that in order to understand how vision is accomplished, some knowledge of optics is absolutely essential, so for the comprehension of the manner in which the voice is produced and sound is heard, a knowledge of acoustics is equally indispensable. Similarly as in the case of vision, attention was continually being called to the distinction between the sensation of sight and the waves of light giving rise to it, so in case of sound, the sensation of hearing must be distinguished from the waves of sound giving rise to it, for what constitutes in us subjectively hearing, is out of us objectively vibration. Our knowledge of sound must be then like that of light, etc., of all knowledge only relative, depending upon the vibrations, and the extent of the susceptibility of the auditory apparatus being impressed by the same. Let us consider first then, how sound is produced in general, and more especially by the larynx, and then turn to the consideration of how it is appreciated by the brain through the ear and auditory nerve. The sensation of sound, or more properly of musical sound as contrasted with mere noise, is due, as we shall see presently, to the periodic rhythmic vibratory wave-like oscillation of the sounding or sonorous body, being transmitted by an elastic medium, usually the air, to the ear, noise being due to the oscillations being transmitted in an unperiodic, irregular manner. The drawing of the bow across the strings of a violin gives rise in us to what we call music, the shaking of a box containing nails, chisels, files, etc., to noise, the auditory nerve being affected in the one case by oscillations following each other in a regular, orderly sequence, and in the other by irregular, disorderly oscillations following each other in no sequence at all. The effect of noise upon the ear has often been compared to that of flickering light upon the eye, the painful experience in both cases being due to the sudden, abrupt, and irregular stimulation of the auditory and optic nerves respectively. Nevertheless, the difference between noise and sound is not an absolute one, being rather one of degree than of kind, as shown by the noise due to the rattling of a carriage over stones, becoming a musical sound as soon as the oscillations become rhythmical and regular in character. Let us endeavor to explain now by a few simple illustrations, what is meant by periodical rhythmical vibrations, to which the sensation of sound has just been said to be due. Let us suppose, for example, that a number of persons are standing in a row, one behind the other, each individual's hands resting against the back of the one in front of him, and that the individual at the one end of the row be suddenly pushed from behind, forward against the individual standing in front of him, the latter in turn will be pushed against the individual standing in front of him, and so

through the whole row until the last individual will be pushed forward. Further, let us suppose that the push be not very violent, and that the individual at the one end of the row first pushed forward regains his erect position, and then the second regains his, and so on through the whole row until the last man at the other end of the row regains his position, it is evident that though each individual person may have swayed to and fro, oscillated pendulum-like through a very small fractional part of the distance through which the push has passed, the push itself or the wave may have been transmitted through a long row of individuals, a hundred or more. Conceive the first individual body, the last individual of the row, to be the tympanic membrane of the ear, the intermediate individuals of the row, laminae of air or of any other elastic medium, and we can readily picture to ourselves what is taking place in the air, as the wave giving rise to the sensation of sound passes from the sounding body to the ear. The conditions being strictly analogous in both cases, each lamina of air being pushed forward against its neighbor, through the elasticity of the air, after giving up its motion to the next lamina will recoil again, and just as in the case of the individuals in the row, the more rapid the to and fro motion of the laminae of the air, the greater the velocity of the push transmitted through the row and of the sound wave through the air. On account of the importance of thoroughly understanding the manner in which the sound is propagated in air, let us consider a little more particularly the case in which it is propagated, through a tube of indefinite length. Let A B (Fig. 496) be a tube filled with air, the temperature and pressure

FIG. 496.



To illustrate propagation of sound in air.

being constant, and let us suppose that P be a piston, oscillating rapidly from C to D, then as the piston passes from C to D, it condenses the air in the tube, the condensation, however, not extending at once throughout the whole tube, but on account of the great compressibility of the air only to the extent D E. As the piston, however, then passes from D back to C, the air in contact with its posterior face expands and becomes rarefied, and by the time that the piston reaches C, the air has become rarefied to an extent (E D) exactly equal, but opposite in direction to that of the previous condensation (D E). Supposing the tube A B to be divided into equal parts (D E, E F, F C, G H), etc., it is also evident that by the time the condensation beginning, at say E, reaches F due to the forward movement of the piston from C D, condensing D E, that the rarefaction beginning at E due to the backward motion of the piston from D to C will reach D, and that the forward condensation E F and backward rarefaction E D are equal and opposite in direction. The condensed and rarefied laminae of air (E F, E D) so



produced during the forward and backward movements of the piston, constitute a wave, a vibration, an undulation, just as the to and fro motion of a pendulum constitutes a vibration, the length of the sonorous wave or vibration being the distance traversed by the sound during the complete vibration, or to and fro movement of the vibrating body causing it. In France, however, a vibration is considered as being either the to or fro movement, not both, that is to say, each English vibration is equal to two French ones. By a vibration we shall always mean the double vibration equal to two single French ones. That is to say, as the piston passes from C to D, the sound travels from D to E, and as the piston passes back from D to C, the sound passes on from E to F. It need hardly be added, that the length of the undulations will be less in proportion to the rapidity with which they follow each other, and that though the to and fro movements of the individual particles of the air giving rise to the condensations and rarefactions may be very slight, and the undulations long or short, few or many in a given time, the sound wave itself may be transmitted to a great distance.

Such being the manner in which a sound-wave is propagated in a cylindrical tube, there will be no difficulty in comprehending how sound-waves are propagated in an uninclosed medium, if we only conceive each molecule of the vibrating body as acting as the piston in the tube, a series of waves alternately condensed and rarefied being then generated around each centre of vibration, the sound radiating in all directions, like the waves of water spreading out upon the surface from some point of disturbance—the intensity of the same gradually, therefore, in both instances diminishing. That sounding bodies are actually vibrating can be readily demonstrated. In the case of strings it is a mere matter of observation, the vibrations being so apparent as to be visible to the naked eye. It will be remembered, also, that we made use of the traces due to the vibration of a reed or tuning-fork to determine small intervals of time, and, indeed, by such graphic methods we are accustomed to test the accuracy of our standard tuning-forks. Apart, also, from the thrill experienced when a sounding bell is touched, its vibrations are made visible indirectly at least by the brisk to-and-fro movement of pith balls placed in contact with it. The vibrations of a sounding glass plate can also be rendered visible, as first shown by the celebrated Chladni<sup>1</sup> by sprinkling sand upon its surface, the sand only remaining at rest upon the part of the plate not in vibration, and disposing itself in characteristic lines according to the shape of the plate and the character of the sound. It has already been mentioned that the vibrations of sonorous bodies can only give rise to the sensation of sound in us by the intervention of an elastic medium interposed between the ear and the vibrating body, and vibrating with the latter. While this medium is usually the air, the waves of sound are also transmitted through gases, vaporous liquids, and solids. A diver at the bottom of the water can hear the sound of voices on the bank; the scratching of a pen at one end of a piece of wood is heard at the other end; while the earth con-

<sup>1</sup> Die Akustik, S. xvi,

ducts sound so well that if at night the ear be placed upon the ground, the steps of horses, or other sounds or noise can be heard at a great distance off. That the waves of sound are not propagated in vacuo, as first shown by Hawksbee,<sup>1</sup> can be very easily demonstrated by means of the apparatus constructed by Queen & Co., for the author, which consists of an air-pump and receiver standing upon wadding, and a bell, the hammer of which is made to strike by clock-work set going by the raising of a detent passing through the top of the receiver. The bell, etc., having been placed within the receiver, the air from the latter exhausted by the pump, and the hammer made to strike, no appreciable sound will be heard until the air is allowed to pass into the receiver. By allowing hydrogen gas, which is fourteen times lighter than air, to pass into the receiver, and by which the air is rendered very much more attenuated, such a perfect vacuum is obtained that not the slightest sound is heard, even though the ear be placed against the bell itself. The experiment just described is not only a very striking one, as proving that sound is not transmitted in vacuo, or a very attenuated atmosphere, but it illustrates the difference between the cause of sound and the sensation of sound, since, though the hammer may be seen striking the bell and causing it to vibrate, no sound is heard as long as the vacuum is maintained, there being no intermediate medium to transmit the vibrations of the bell to the ear. Sounds, however produced, whether by strings, reeds, tuning-forks, bells, plates, etc., are distinguished by their intensity, pitch, and quality, and as these differences in the character of sounds must be thoroughly appreciated in order to understand how the voice is produced, and sounds are heard, let us endeavor, therefore, to explain them now a little in detail.

#### INTENSITY OF SOUND.

By the intensity of sound is meant the loudness of sound. We hear one sound louder than others because the particles of air set in motion by the sounding body strike the tympanic membrane of the ear harder in the one case than another. Just as the force with which a ball strikes a target can be shown on mechanical principles to be proportional to its weight and the square of the velocity with which it is moving, so the force with which the air particles strike the tympanic membrane can be shown to be proportional to the square of the maximum velocity with which it is moving. The intensity of a sound depends, however, on the density of the air in which the sound is generated, and not on that of the air in which it is heard. Thus, while a cannon fired in a valley may be heard at the top of a high mountain above, the same cannon fired at the top of the mountain will not be heard in the valley below, the sound generated in the dense air of the valley being louder than that generated in the rare air on the top of the mountain. The intensity of the sound is also proportional to the square of the amplitude of the vibration, the amplitude being the width of swing, the distance through which the air particle moves to and fro when the sound-wave passes it.

That such is the case can be readily shown by means of vibrating

<sup>1</sup> Phil. Trans., vol. xxiv p. 1004.



cords; for if the latter are long, the oscillations being visible to the eye, it will be seen that the sound becomes feebler in proportion as the amplitude of the oscillation decreases. The intensity of sound is modified by the distance of the sonorous body from the ear, varying inversely as the square of the distance; that is to say, for example, the intensity of the sound of a bell, situated at a distance of 20 yards from the ear, would be only one-fourth of the intensity of the same bell if situated at 10 yards from the ear, or half the distance; or, what is the same thing, the intensity of four bells, situated at a distance of 20 yards, is the same as that of one bell situated at a distance of 10 yards from the ear, supposing, of course, that the bells are all of the same size, and other conditions equal. That the intensity of the sound must diminish in the above ratio—that is, as the square of the distance—will become evident when it is borne in mind that, as the spherical waves of sound radiate outward from the centre of disturbance toward the periphery, the mass of air set in motion must be continually augmented as the squares of the distance from the centre, the areas of circles being to each other as the squares of their radii. The matter affected increasing then as the square of the distance, the intensity of the sound must diminish in the same ratio. If, however, the wave of sound be propagated in a tube, lateral diffusion being prevented, as in Fig. 496, then the sound can be transmitted through great distances with very little diminution in intensity; thus Biot found that a person whispering at one end of one of the empty water-pipes of Paris, a tube 3120 feet in length, could be heard at the other end, and that the firing of a pistol at one end of the tube put out a lighted candle at the other. The intensity of sound is modified by the condition of the atmosphere, sound being better propagated in calm than in windy weather; in the latter case, however, sound is better heard when transmitted in the direction of the wind than in the opposite direction. Finally, the intensity of sound is very much increased by the proximity of a sonorous body. Hence, the association of sounding-boxes with strings, as in the case of the violin, guitar, etc., the increase in the loudness of the sound being then due to the fact that the box and air within it vibrate in unison with the strings as we shall endeavor presently to explain. The distance at which sounds are heard, depending upon their intensity, may be very great; thus, it is said that the report of the volcano at St. Vincent was heard at Demerara, 300 miles off, and the firing at Waterloo at Dover.<sup>1</sup>

#### PITCH OF SOUND.

Sounds are distinguished, as already mentioned, not only by their intensity or loudness, but by their pitch or height. The pitch of a sound can be shown to depend upon the number of vibrations made by a sounding body in a given time—a second, for example—sounds of low pitch being due to the aërial vibrations impinging upon the tympanic membrane following each other slowly, those of high pitch to the aërial vibrations following each other rapidly. Thus, for example, the pitch

<sup>1</sup> Ganot: *Physics*, trans. by Atkinson, p. 175. London, 1870.

of the sound of a string four feet in length, sufficiently tensed, and of a given density and thickness, vibrating 128 times in a second ( $\text{Do}^2, \text{Ut}^2, \text{G}^2, \text{C}$  of piano), is low as compared with that of one two feet in length, vibrating 256 times in a second ( $\text{Do}^3, \text{Ut}^3, \text{C}^3, \text{c}^1$ ), or an octave above.<sup>1</sup> In the same way, the pitch of the sound of an organ-pipe four feet in length due to 128 vibrations per second ( $\text{Do}^2 \text{Ut}^2$ ) is low as compared with that of the sound of one two

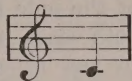
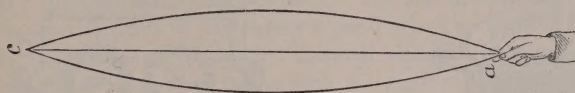
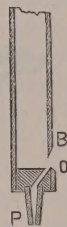


FIG. 497.

FIG. 498.



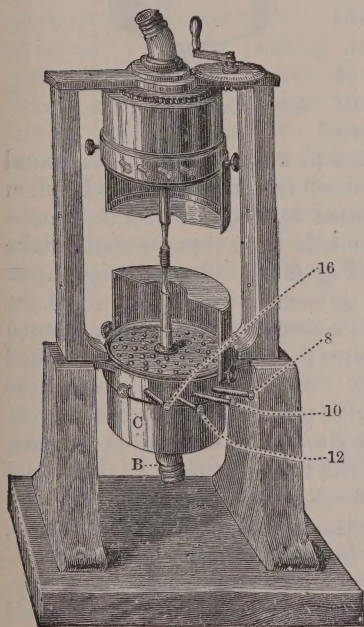
Vibration of string. (TYNDALL.)



Organ pipe.

feet in length, due to 256 vibrations per second ( $\text{Do}^3 \text{Ut}^3$ ) or the octave above. It may be mentioned in this connection that, while in the case of the string it is the vibrations of the latter (Fig. 497) that give rise to the ærial vibrations affecting the auditory apparatus, in the case of the organ-pipe it is to the vibrations of the enclosed column of air that the ærial vibrations are due, as the

FIG. 499.



Helmholtz double siren.

current of air forced by the bellows through the mouth P B of Fig. 498 of the pipe in striking against the upper bevelled lip B, produces a shock, the air issues from the embouchure or space between the lips in an intermittent manner, the pulsations so produced in being transmitted to the air enclosed within the pipe in turn set it into vibration, which causes the sound. It will be observed, also, as might have been anticipated on mechanical principles, that the number of vibrations, both in the case of the string and pipe, are inversely as the lengths, the number of vibrations in both cases being doubled by halving the lengths, since, in the latter case, the amount of work to be done being one-half, it can be done in half the time, or double the work can be done in the same time. The distinction between intensity or loudness and pitch or height must be carefully borne in mind, being, as just shown, due to

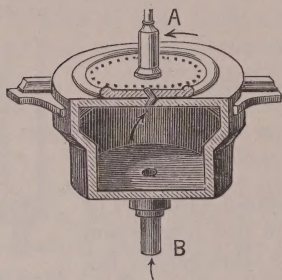
entirely different causes; a sound, therefore, may be a loud one, and yet be low in pitch; and, on the other hand, a sound may not be a loud

<sup>1</sup> If the 5th A of the piano be tuned to vibrate 440 vibrations per second, instead of 426 times as assumed in text, then the middle C or  $\text{Ut}^3$  will vibrate 264 times, and the lowest C 33 times per second.



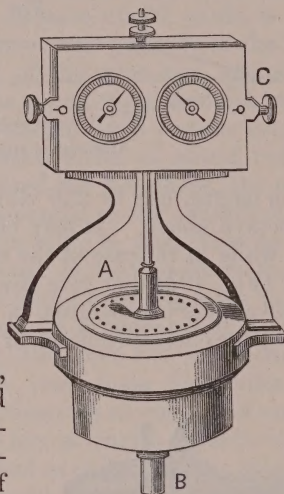
one, and yet be high in pitch. In sounding the long string and long organ-pipe, apart from the intensity of the sound, and from the pitch of the note  $\text{Do}^2\text{Ut}^2$ , 128 vibrations per second, the same, therefore, in both cases, another and very marked difference is appreciable, and that by not especially musical ears, viz., the character or quality of the sound. Before considering, however, the quality of sound, or that in

FIG. 500.



Showing oblique opening in siren  
of Cagniard de la Tour.

FIG. 501.



Siren of Cagniard de la Tour.

which the sound of a violin, for example, differs from that of a piano, and the sound of the latter from the sound of the organ-pipe, or, in general, that which distinguishes the sounds of different kinds of musical instruments, let us first endeavor to explain how, by means of the siren, we are able to determine the number of vibrations to which the pitch of a sound is due. The siren—so called on account of its emitting sounds when under water in its original form as invented by Cagniard de la Tour—is apparently a much more simple instrument than that we shall make use of, or the double siren of Helmholtz (Fig. 499). The principle upon which both instruments are constructed is, however, the same, since the siren of Helmholtz consists of two Dove sirens, the Dove siren in turn differing from that of Cagniard de la Tour (Fig. 501) in being provided with four series of orifices instead of one. Such being the case, let us begin our description of a double siren with that of a single Dove siren. Suppose, for example, that the lower Dove siren (Fig. 499) be taken apart, it will be seen that the tube B leads into the brass cylinder C, the top of which is closed by a brass plate *a b*, perforated with four series of holes disposed concentrically, the outermost series containing 16, the next 12, the next 10, the next 8 orifices, the latter being opened or closed, respectively, by pressing in or pulling out the keys numbered correspondingly. It will also be seen that the brass disk, receiving in its centre the steel axis *x*, is also perforated with 16, 12, 10, and 8 orifices, disposed concentrically at the same distance from the centre, and with the same intervals between them as those on the top of the cylinder C, the only difference between the two sets being that those passing through the top of the cylinder C, while oblique in direction (Fig. 500), are oppositely inclined to those passing also obliquely through the brass disk *d e*.

The two sets of orifices being so disposed to each other if air be forced by a pair of bellows through the tube B into the cylinder C, the air will issue from the latter not vertically but in side currents, which in impinging against the sides of the orifices of the disk will drive the disk around the axis  $x$ , held upright by means of a steel cap brought down on its upper end. As the disk turns around, its orifices, coming alternately over the orifice of the cylinder C and over the intervening spaces, the continuous current of air passing through the cylinder C is carved into discontinuous puffs, which at first follow each other so slowly that they may be counted. As the motion of the disk, however, increases the puffs of air succeed each other so rapidly that the air links them together as continuous musical notes, whose pitch can then be at once shown to depend upon the number of puffs of air or vibrations, by simply increasing or diminishing the rapidity of the rotation of the disk, the pitch of the note rising or falling accordingly. In order, however, to determine the number of puffs of air issuing from the orifices in a given time, a second, for example, they must be recorded. This is accomplished by providing the axis  $x$  at its upper part with a screw  $s$  (Fig. 502) which works into a pair of toothed wheels, the latter rotating as the disk and its axis turn, the number of rotations being indicated by the hands on the dial plates (omitted in Fig. 499, but represented in Fig. 501), the hand of one dial plate making an entire revolution while that of the other passes over but one division of the graduated circumference. The process of recording can be started or stopped by simply pushing a button, which throws the wheel-work just mentioned into or out of action. In order, now, to show how by means of the siren we determine that the note  $Do^3$ ,  $Ut^3$  emitted by the string or organ-pipe two feet long, is due to the vibrations following each other at the rate of 256 vibrations a second, we force the air from the bellows through the cylinder C until the disk rotates so rapidly that the sound produced by the siren is in unison with that emitted by the string or organ-pipe sounded at the same time. The sound of the siren and the string or pipe being then in perfect unison, we push the button and so set going the recording mechanism and let the siren sing for just one minute, then instantly stopping the recording, we observe by the hands of the dial plate the number of rotations the disk  $de$  has made in that time. It will be found that the number is just 960, dividing this by 60 the quotient, or 16, will be the number of times that the disk has rotated in one second, but since 16 orifices were open in one rotation of the disk 16 puffs of air issued in succession from the siren, and consequently during 16 rotations 256 puffs of air. As the note  $Do^3$ ,  $U^3$  produced by the siren was due to the number of puffs or vibrations of air, and as the note of the siren was in unison with that due to the sounding of the string or pipe, the latter, or  $Do^3$ , must be also due to the same number of vibrations, viz., 256 vibrations per second. It will be remembered that while the outermost series of orifices, those which in the preceding experiment were supposed to be open, are 16 in number, the innermost series of orifices are only 8 in number. If the latter now be opened as well as the former by pushing in the key numbered 8, then two sounds will be simultaneously emitted by the siren, one of which,



Do<sup>3</sup>, is due, as before, to the rate of vibration being 256 per second, the other Do<sup>2</sup> an octave below, the rate being just half, or 128 vibrations per second, the air issuing from 8 orifices during one rotation of the disk, instead of from 16, as in the former case. The innermost and outermost series of orifices being open, then the rate of vibration of the two sounds is as 1 to 2. From what has just been said, it is evident, without further explanation, that if the innermost series of 8 orifices and the next series to it of 10 orifices be open, then the rate of vibration will be as 4 to 5—that is to say, of the two notes produced by the siren simultaneously, if one be Do<sup>2</sup>, due to 128 vibrations per second, the other note will be Mi<sup>2</sup> E<sup>2</sup>, due to 160 vibrations per second, and if the innermost series of 8 orifices and the third series from within outward, that of 12 orifices, be both open, then the rate of vibration of the two sounds will be as 2 to 3—that is, if Do<sup>2</sup> be one of the two notes heard simultaneously the other note will be Sol<sup>2</sup> G<sup>2</sup>, due to 198 vibrations per second. It follows, therefore, that if the three innermost series of orifices, 8, 10, and 12, be open we will obtain the major chord Do<sup>2</sup> E<sup>2</sup> G<sup>2</sup> Do<sup>2</sup> Mi<sup>2</sup> Sol<sup>2</sup>, and if in addition at the same time the outermost series of 16 orifices be open C<sup>2</sup> E<sup>2</sup> G<sup>2</sup> C<sup>3</sup>, which, as produced by the siren, is quite musical. The construction and manner of using a single Dove siren being now understood, there will be no difficulty in comprehending that of Helmholtz, it consisting, as already mentioned, of two dove sirens. It must be mentioned, however, that the outermost series of orifices in the lower of the two sirens are 18 in number instead of 16, as in the single Dove siren we have just described, and that the orifices in the four series of the upper siren are respectively 9, 12, 15, and 16 in number. If, therefore, we wish to obtain by the double siren the major chord C<sup>2</sup> E<sup>2</sup> G<sup>2</sup> and C<sup>3</sup> at the same time, the series of orifices 8, 10, and 12 must be opened in the lower siren, and the series of 16 orifices of the upper siren, the air being allowed, of course, to pass from the bellows through both sirens, the number of rotations of the disks being recorded in the same manner as already described by wheel-work attached to the axis common to the two sirens, and omitted for simplicity in Fig. 499. It will be observed that the double siren is provided with resonance boxes the half of each of which has been removed in the figure, which greatly intensifies the fundamental sound. The upper siren is also connected with a toothed wheel and pinion turned by a handle, by which we are enabled to rotate the cylinder of the upper siren as well as the disk, the handle, etc., being so disposed that if it be turned to the right the orifices in the cylinder and in the disk will then pass over each other more quickly than if the cylinder was at rest, and if in the reverse direction more slowly, the pitch rising in the one case, the puffs succeeding each other then more rapidly, and falling in the other, following more slowly. The use of the dial and index underneath the handle will be illustrated hereafter. It is needless to say that by doubling all parts of the siren, etc., as done by Helmholtz,<sup>1</sup> that many varied combinations can be introduced, and that the general usefulness of the instrument has thereby been greatly increased.

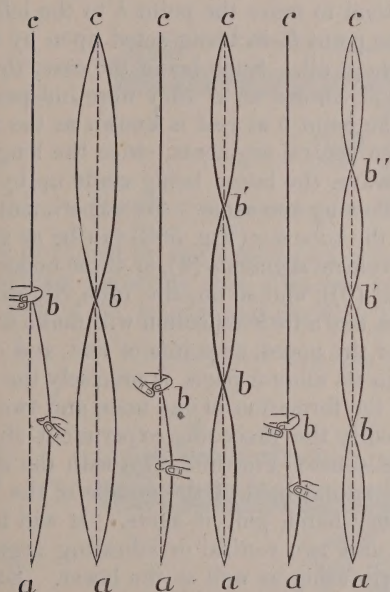
<sup>1</sup> On the Sensation of Tone, transl. by A. J. Ellis, p. 245. London, 1875.

QUALITY OF SOUND.

Every fundamental tone, whether produced by a string, column of air, reed, etc.—that is, a sound due to the string, for example, vibrating through the whole of its length (Fig. 497), may be accompanied by partial tones or overtones<sup>1</sup> due to the string vibrating through the half, third, fourth, etc., of its length (Fig. 502, (2), (4), (6)), and since the overtones, accompanying and reinforcing the fundamental tone, due to the sounding of the string of one instrument, are not the same as those of another, or if in part the same, are then more or less accentuated, there arises in consequence a difference in the character of the sound as produced by the two instruments, very appreciable, even by unmusical ears, which is called their quality. Thus, for example, the sound of the string of a violin may be as loud as that of the piano, or of that of the vibrating column of air of the organ-pipe, or of that of the vibrating reed of the oboe, the pitch of the particular note emitted by the four instruments may be the same, the number of vibrations per

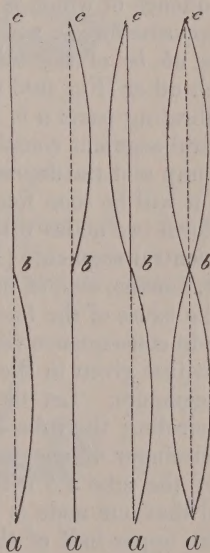
FIG. 502.

FIG. 503.



(1) (2) (3) (4) (5) (6)

Formation of nodes and ventral segments. (TYNDALL.)



(1) (2) (3) (4)

Vibrations of tube. (TYNDALL.)

second to which the note is due being equal in all four instances, and yet no one fails to appreciate the difference in the character or the quality of the sound, the overtones reinforcing the fundamental note

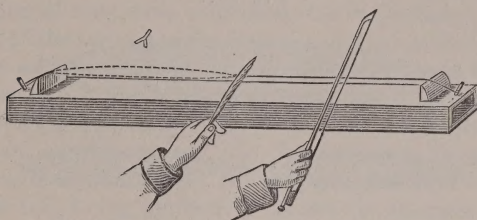
<sup>1</sup> By the 1st, 2d, and 3d overtones, etc., will be meant in this chapter, tones due to vibrations whose rates are twice, three, or four times as rapid as that of the fundamental tone.



being different in each instance. Inasmuch, however, as the thorough understanding of the conditions upon which the quality of sound depends is not only important, but absolutely essential, in comprehending the manner in which the vowels are produced by the larynx, for example, let us endeavor to explain a little more in detail how these partial vibrations, to which the overtones are due, come to be superimposed upon the fundamental one, and how their presence can be detected. Let *ca* (Fig. 503) represent a long India-rubber tube fixed at the one end, and free at the other. By taking hold of the free end, stretching the tube a little, and properly timing the impulses, the tube can be made to swing to and fro, to vibrate as a whole, as represented in Fig. 497. Stop the motion, and now, by a jerk, raise a hump upon the tube, the hump will be observed to run along the tube *ab*, *bc* (Fig. 503, (1), (2)), and having reached the fixed end of the tube *c*, will then run back again, but in the reverse direction. But just as the latter *cb* (3) starts at *c*, let the tube be jerked again, so as to start the hump *ab* (3) at *a*, then by the time that the foremost part of the hump beginning at *c* arrives at *b*, that beginning at *a* will also have reached *a*, the effect of which will be that the point *b* will remain at rest. For the hump *ab* (3) in moving on to *c* must tend the point *b* to the right, and the hump *cb* moving on to *a* must tend to move the point *b* to the left, the consequence of which is, that the point *b*, in being acted upon by equal and opposite forces, will not move at all. Such being the case, the two halves, *ab*, *bc* of the tube *bc*, will vibrate as if they were independent of each other (Fig. 503 (4)). The point *b* at rest is known as the node, the vibrating parts *ab*, *bc* as the ventral segments, twice the length of a ventral segment constitutes a wave, the latter being made up by both the hump and the depression following the same. By experimenting a little, it will be soon found that the tube *ac* (Fig. 502) can be so swung as to form two nodes with three ventral segments (4), or three nodes with four ventral segments (Fig. 502, (6)), and so on, the tube vibrating in thirds, fourths, etc., of its lengths, and a little reflection will make it clear that the cause of the formation of the nodes, or points of rest, and of the string in consequence vibrating in its aliquot parts, is precisely the same as that just given in the case of the formation of one node and two ventral segments. Let us now modify the preceding experiment slightly by encircling the tube *ac* at its centre (Fig. 502, (1)) with the thumb and forefinger of one hand, and taking hold of the middle of the lower half of the tube *ab* with the other hand, pull it aside. It will be observed that one node is formed, and two ventral or vibrating segments (2), the upper half of the tube vibrating as well as the lower. Experimenting in this way, but encircling, however, the tube at one-third (3) or one-fourth (5) of its length, and pulling the lower third (3) or lower fourth (5) of the tube away by seizing them, respectively, at their centres, the tubes will be oscillated, so that two nodes with three ventral segments (4), or three nodes with four ventral segments (6), will be formed, as the case may be, the vibrations of the string through the space encircled by the thumb and finger, a distance of one inch, acting upon the upper part of the tube exactly as the hand acted when it caused the tube to swing as a whole. In precisely the same manner,

by placing a feather (Fig. 504) upon the centre of the stretched violin-string, just as we encircled the tube with the thumb and finger, and

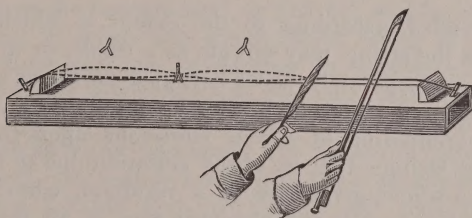
FIG. 504.



Formation of one node and two ventral segments. (TYNDALL.)

drawing a bow across the centre of the half of the string instead of pulling it aside with one hand, the string will be made to vibrate in

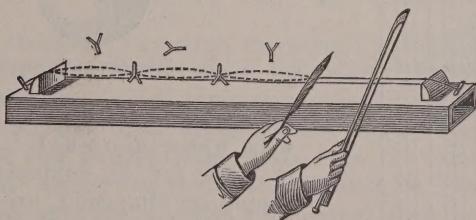
FIG. 505.



Formation of two nodes and three ventral segments. (TYNDALL.)

halves, as shown by the little paper rider being thrown off. Similarly, by touching the string with a feather at a third (Fig. 505), or a fourth (Fig. 506) of its length, and drawing the bow across the centre of the

FIG. 506.



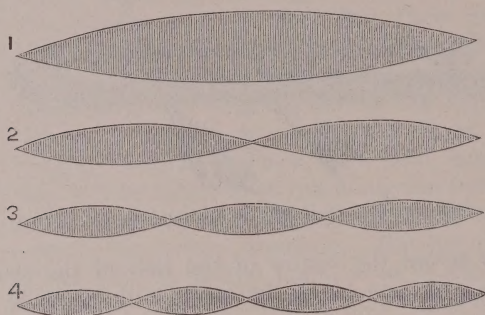
Formation of three nodes and four ventral segments. (TYNDALL.)

right hand third or fourth, the string will vibrate in thirds or fourths, two nodes with three ventral segments, or three nodes with four ventral segments being formed, as shown by the two or three red paper riders placed upon the vibrating parts being tossed off, and the one or two blue ones remaining on the string being situated at the nodes, or points of rest. A beautiful way of demonstrating the presence of nodes and ventral segments, occasionally made use of by the author in addressing a large audience, is to place a string connected at one end with the



prong of a tuning-fork, and at the other with a peg, by which it can be loosened or tightened in front of the calcium light lantern, an appearance such as that represented in Fig. 507 being presented when

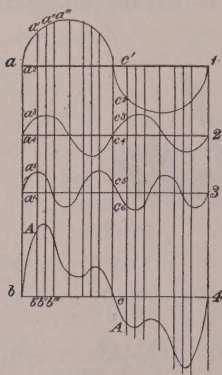
FIG. 507.



Nodes and segments of a vibratory string as shown by lantern.

the fork is sounded, according to the extent to which the string is tensed. While the string may vibrate as a whole, or in halves, thirds, fourths, fifths, etc., separately, as we have just shown, as a matter of fact, the string usually in vibrating breaks up, so to speak, into its aliquot parts, the superimposing of which vibrations upon the fundamental vibration of the string—that is, of the vibration due to the swinging of the string, as a whole, gives rise to a resultant vibration, which has been shown to be equal to the algebraic sum of all the vibrations,<sup>1</sup> as represented in Fig. 508, in which the lower curve represents the compound vibration resulting from the blending of the three upper curves,

FIG. 508.



Compound waves. (MCGREGOR ROBINSON.)

FIG. 509.



Resonator of Helmholtz.

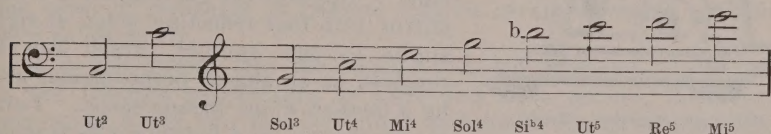
representing, respectively, simple vibrations, whose ratio is as 1, 2, 3. Of course, it must not be supposed that sounds, simple or compound, are due to curves like those depicted in Fig. 508; the latter are simply graphic representations of waves of sound, which, as we have seen, consist of condensations and rarefactions of the air. That the tone due to the sounding of a string of the piano, such as

$\text{Do}^2$ ,  $\text{Ut}^2$ , vibrating 128 times per second, is not a simple, but a compound tone, will be appreciated by a trained musician, whose sensitive

<sup>1</sup> Helmholtz, *op. cit.*, p. 43.

ear enables him to distinguish some at least of the overtones accompanying the fundamental tone. Any one, however, can convince himself that such a tone as that of  $Ut^2$  sounded by the piano, as elicited by singing the corresponding note, is a compound one, resulting from the blending of the fundamental tone with overtones, the latter being due to the partial vibrations of the string, as the former is to the oscillating of the string as a whole, by adapting to his ear in succession each one of the series of nine resonators, of which one is represented in Fig. 509, devised by Helmholtz,<sup>1</sup> and so constructed as to intensify the sound of each particular overtone accompanying the fundamental tone, that overtone being then heard alone. Thus, for example, the first and largest resonator, marked  $Ut^2$ , being applied to the ear, let the note  $Ut^2$  be sounded due to 128 vibrations a second; the first overtone or harmonic, or the octave above  $Ut^3$ , 256 vibrations per seconds, will be heard, due to the string vibrating in halves, the sound distinctly heard with the resonator being the same as if the note  $Ut^3$  had been sounded.

Applying the second or next largest resonator, marked  $Sol^3$ , to the ear and sounding the  $Ut^2$  string on the piano the second overtone, the twelfth above the fundamental, or  $Sol^3 G^3$ , will be heard, due to the string vibrating in thirds, the sound heard being the same as if the note  $G^3$  had been sounded. Adapting in succession the remaining resonators gradually diminishing in size, and marked respectively  $Ut^4$   $Mi^4$ ,  $Sol^4$   $Si^b4$   $Ut^5$ ,  $Re^5$   $Mi^5$ , the 3d, 4th, 5th, 6th, 7th, 8th, and 9th overtones due to the string or harmonics will be heard vibrating in fourths, fifths, sixths, etc., the sounds heard with the resonators being the same as if the notes  $Ut^4$   $Mi^4$   $Sol^4$   $Si^b4$   $Ut^5$   $Re^5$   $Mi^5$  had been separately sounded, or as expressed in musical notation as follows,  $Ut^2$  being the fundamental tone:



It is obvious, therefore, why when the notes  $Ut^3$   $Sol^3$   $Ut^4$  are sounded on a musical instrument at the same time with  $Ut^2$ , the resulting sound should be harmonious, since these three sounds reinforce respectively the first, second, and third overtones due to the string vibrating in halves, thirds, and fourths respectively. In the same way,  $Mi^4$   $Sol^4$   $Si^b4$   $Ut^5$   $Re^5$   $Mi^5$  reinforcing the overtones due to the string  $Ut^2$  vibrating in fifths, sixths, sevenths, eighths, and ninths, when sounded with  $Ut^2$ , will also give a harmonious sound.

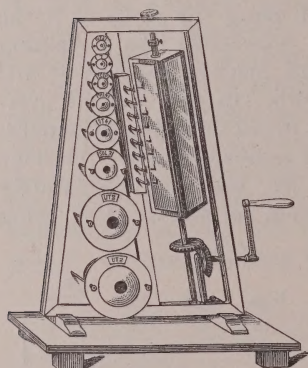
Having described the manner in which partial vibrations are formed, and how in being superimposed upon the fundamental vibration a resultant vibration arises, and how the overtones due to the partial vibrations in being blended with the fundamental tone due to the fundamental vibration give rise to a compound tone, it becomes evident without further explanation, that by means of the Helmholtz resonators

<sup>1</sup> Op. cit., p. 68



we can analyze any sound, and demonstrate whether it be a simple or compound one, and, if the latter, what overtones are present, and in this way show on what the quality, timbre, or klangfarbe of the sound depends. Thus, for example, the quality of the sound of the piano, as compared with that of the violin, depends upon the fact that in the case of the latter, when bowed, though the first six overtones or harmonics are present, as in the case of the piano. they are so faintly sounded as to be overpowered by the seventh, eighth, ninth, and tenth overtones. The overtones in the case of an open pipe are not the same as in the case of a closed one; those of the clarinet differ from those of the oboe, and so through the whole range of orchestral instruments. Inasmuch, however, as in addressing a large audience, from the nature of the case, it is impossible for each one individually to make use of the resonators and satisfy himself of the existence of overtones upon which the quality of a sound depends; the author is accustomed to demonstrate the same by means of Kœnig's manometric apparatus.<sup>1</sup> The latter (Fig. 510) consists of a frame supporting fourteen resonators

FIG. 510.



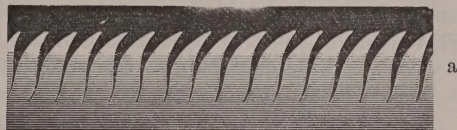
Manometric apparatus. (KœNIG.)

each of which leads by a narrow India-rubber tube into a small chamber, completely divided into two, by an India-rubber partition. The posterior part of the chamber is in communication with the resonator, the anterior part provided with a gas jet with a reservoir containing gas, led thither by an ordinary gas pipe. Each resonator is connected in this way with its own gas chamber and burner, the burners being all placed in a row, one above the other. Opposite the gas burners is a long mirror with four reflecting sides, at right angles to one another, which can be revolved on an almost perpendicular axis by a toothed wheel arrangement. Turning on the gas, and lighting it as it issues from the jets in the chambers connected with the resonators, and revolving the mirror, the light reflected from the surfaces of the latter appears as continuous bands. If, however, the air in any one of the resonators be thrown into vibration, then the India-rubber partition of the chamber separating, on the one hand, the air continuous with that of the resonator, and, on the other, the gas, will vibrate, and the gas and flame thrown into agitation, the particular band of light, the corresponding band of light, becoming segmented. Let now a tuning fork  $Ut^3$ , vibrating 256 times a second, be sounded in front of the apparatus; at once the flame in connection with the resonator marked  $Ut^3$ , will become segmented, but the remaining flames will still appear as continuous bands of light, since if the tuning fork be properly bowed the sound produced will be a pure, simple tone, unaccompanied with overtones. Let now, however, the  $Ut^3 Do^3$  of the piano, or an

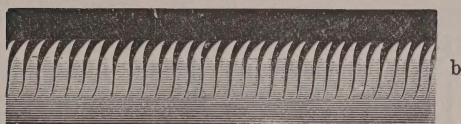
<sup>1</sup> Rudolph Kœnig, *Quelques Experiences d'Aoustique*, p. 73. Paris, 1882.

open organ pipe two feet long, giving, therefore, the same fundamental note, be sounded, and immediately some of the remaining bands of light will become segmented, as well as the one connected with the resonator marked  $U^3$ , since the air of the resonators with which they are in connection has been thrown into vibration by the particular overtones present, as, for example, in Fig. 511, a, b, respectively, representing the

FIG. 511.



Fundamental note.

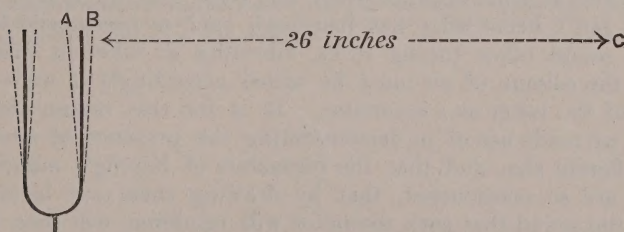


Octave of preceding.

flames due to the fundamental and octave above it. In this way an optical demonstration can be given of the fact that the quality of the note of any musical instrument depends upon what particular overtones or harmonics accompany the fundamental, and, as we shall see presently, of the manner in which the vowel sounds are produced by the human voice. As it is important that the manner in which resonators reinforce or intensify sounds should be understood, a brief account of the cause of resonance in general may be as appropriately considered here as elsewhere.

It is well known that the velocity with which sound travels in air at the freezing temperature is 1090 feet in a second, the velocity increasing about two feet for every additional degree of heat, Centi-

FIG. 512.



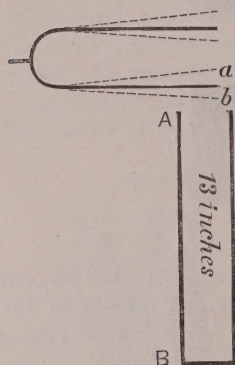
Vibrating of tuning fork. (TYNDALL.)

grade ( $1.8^{\circ}$  F.). Let us suppose that the temperature of the surrounding atmosphere be  $8.5^{\circ}$  Cent. ( $47.3^{\circ}$  F.), and that a tuning fork vibrating 256 times per second be sounded; it is obvious that if, at the



end of the second, the sound has reached a distance of 1109 feet, then each vibration must have been 52 inches long, since 52 by 256 is 1109 feet, and as a vibration or wave of sound consists, as we have seen, of a condensation and rarefaction, the condensation and rarefaction must have been both just 26 inches in length—that is to say, as the prong of the tuning fork (Fig 512) moves from A to B, a distance of perhaps the one-twentieth of an inch, it generates the one-half of the sonorous wave, the condensation, the foremost point of which reaches the point C, a distance of twenty-six inches, at the some instant that the prong of the fork reaches B, and that as the forward motion is being

FIG. 513.



Tuning fork vibrating in unison with jar.

delivered up to the air succeeding C—that is, as the prong of the fork moves back from B to A, the other half of the sonorous wave, is generated, the rarefaction. Such being the case, let the tuning fork now be sounded over a jar (Fig. 513), of which the column of air within, from top to bottom, measures just thirteen inches, or one-fourth the length of the vibration or wave due to the sounding of the fork. It follows from what has just been said, that during the time the prong of the fork moves from *a* to *b*, the condensation, the air which it produces runs from the top of the jar to the bottom, thirteen inches, and from the bottom to the top, thirteen inches, or twenty-six inches in all, the reflected wave reaching the prong of the fork just as the latter reaches *b*; and

similarly, that during the time the prong returns to *a* from *b*, the rarefaction to which it gives rise, runs down from the top of the jar to the bottom, and up again, also a distance in all, of twenty-six inches.

The vibrations of the fork being, therefore, perfectly synchronous with the vibrations of the aerial column within the jar, the motion will accumulate in the latter, and spreading out into the room, the sound will be greatly augmented as everyone will appreciate, when the tuning fork is sounded first at some distance from, and then over the mouth of the resonating jar. From what has just been said, it necessarily follows that if we sound other tuning forks, vibrating at different rates, the length of the column of air must be varied accordingly if we wish to make use of the latter as a resonator. It is for this reason that the resonators we made use of in demonstrating the presence of overtones were of different size, and that the resonators of Koenig's manometric apparatus are so constructed, that by drawing them out to varying distances, the sound that each resonator will reinforce, will then be apparent. It was on account of its resonating qualities, that in sounding the bell in a preceding experiment, the latter was placed near the mouth of a jar, by means of which the intensity of the sound was very much increased. The ancients were well acquainted with the efficacy of such aids in intensifying sound, resonant brass vessels being placed, according to Vitruvius, in their theatres to strengthen the voices of the

actors. It is on account of the resonating properties of sounding boards, that the latter are associated with musical instruments, and that the stethoscope also has proved in the hands of the clinician such an aid in the diagnosis of disease by auscultation. It may not prove uninteresting in this connection to mention that the velocity of sound in air was approximately deduced by Newton<sup>1</sup> from the elasticity and density, the velocity being shown to be directly proportional to the square root of the elasticity, and inversely as the square root of the density. The immortal author of the *Principia*, however, failed to take into consideration, as shown afterward by Laplace,<sup>2</sup> that the condensation in giving rise to heat, and increasing the elasticity, thereby increases the velocity, and that the discrepancy existing between the velocity of sound experimentally observed, and as theoretically calculated by Newton, disappears if the calculated velocity be multiplied by  $\sqrt{1.414}$ , or the square root of the ratio of the specific heat of air at constant volume, to that at constant pressure. Thus, if  $V^1$  be equal to the true or observed velocity,  $V$  be equal to the velocity as calculated by Newton, or 916 feet per second,  $CP$  the specific heat of air at constant pressure,  $CV$  the specific heat of air at constant volume, and the ratio of  $\frac{CP}{CV} = 1.414$ , then

$$V' = V \sqrt{\frac{CP}{CV}} \text{ or } V' = 916 \times \sqrt{1.414} = 1090 \text{ feet.}$$

As a matter of fact, however, at the present day the ratio 1.414 per second is obtained by the reverse operation—that is, knowing  $V'$  and  $V$ , evidently then  $\frac{V'^2}{V^2} = \frac{CP^2}{CV^2}$ , from which we obtain the ratio  $\frac{CP}{CV}$

Having shown that sounds are produced by the vibrations of plates, bells, strings, pipes, reeds, membranes, etc., and how the same are distinguished by their intensity, pitch, and quality, let us turn now to the consideration of the larynx, and by means of the principles just established, endeavor to determine what kind of an acoustical instrument the larynx is and how the voice is produced by it.

<sup>1</sup> *Philosophiæ Naturalis Principia Mathematica*, Liber Secundus Propositio xlix. Londini, 1726.

<sup>2</sup> *Mécanique Céleste*, tome iv. p. 87. Bull. des Sciences Soc., Philomatique, 1821, pp. 161–183. Poisson, *Annales de Chimie et Physique*, tome xxiii. 337.

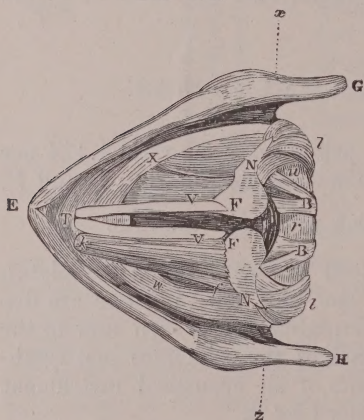


## CHAPTER LII.

### THE LARYNX, AND THE PRODUCTION OF THE VOICE AND SPEECH.

THE larynx, the organ of the voice, situated at the top of the trachea and below the root of the tongue and the hyoid bone, consists of a framework of cartilages, connected by ligaments, provided with muscles, bloodvessels, and nerves, and lined with mucous membrane. The cartilages of the larynx are nine in number, three single and symmetrical pieces, the thyroid, cricoid, and epiglottic, and three pairs, the arytenoid, cornicula laryngis, and cuneiform; the last two pair are, however, very small. The thyroid (Fig. 514), the largest of the cartilages

FIG. 514.

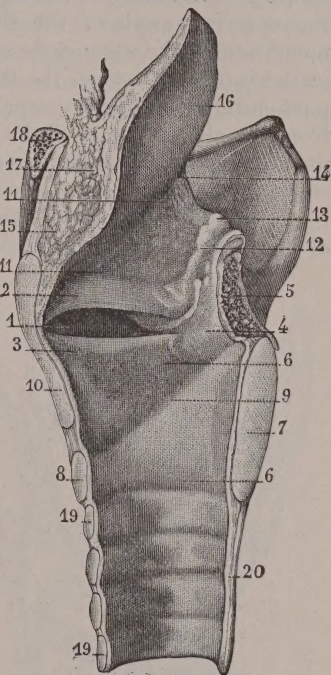


Bird's-eye view of larynx from above: GEH, the thyroid cartilage, embracing the rings of the cricoid, *ru x w*, and turning upon the axis, *x z*, which passes through the lower horns. *N F*, *N F*, the arytenoid cartilages connected by the arytenoideus transversus; *T V*, *T V*, the vocal ligaments; *N X*, the right crico-arytenoideus lateralis (the left being removed); *v k f*, the left thyro-arytenoideus (the right being removed); *N l*, *N l*, the crico-arytenoidei postici; *B*, *B*, the crico-arytenoid ligaments. (CARPENTER.)

of the larynx, consists of two lateral ring-like plates or alæ, continuous in front, but diverging behind. The angular projection in front, surrounded by a deep notch much more marked in the male than in the female, and in some men more than others, is known as Adam's apple, while the blunt processes connected through ligaments with the hyoid bone, into which the posterior angles are prolonged, are called the superior and inferior horns, of which the superior is the larger. The cricoid cartilage, resembling in shape a seal ring, is situated between the thyroid and the first ring of the trachea, with the latter of which it is connected. While quite narrow in front, the cricoid cartilage deepens considerably posteriorly, and at the back part of its upper border, articulates by means of two convex oval prominences with the arytenoid cartilages, and laterally through two circular facets with the inferior horns of the

contain also two small yellowish cartilaginous bodies, the cuneiform cartilages or cartilages of Wrisberg. The remaining cartilages of the larynx, the epiglottis consisting really of fibro-cartilage, somewhat spoon-shaped in form, while free at its broad extremity, is attached at its narrow end by a band of fibro-elastic tissue to the thyroid cartilage within the entering angle of its two halves, and to the tongue, hyoid bone, and arytenoid cartilages by the glosso-epiglottidean, hyo-epiglottidean, and aryteno-epiglottidean folds, respectively. The cavity of the larynx (Fig. 515) is divided by the glottis or rima-glottidis—that is, the long, narrow fissure, running from before backward on a level with the lower part of the arytenoid cartilages—into an upper and lower compartment. The upper compartment commencing with the pharynx by the superior aperture of the larynx, contains the ventricles and the upper or so-called false vocal cords. The lower compartment passes inferiorly into the trachea without any observable constriction between them. The mucous membrane lining the cavity of the larynx, continuous with that of the pharynx and trachea, extending from the epiglottis to the tongue and arytenoid cartilages as the glosso-arytenoid epiglottidean folds, descends from the superior aperture, and is reflected at each side outwardly and upwardly as a pair of pouches, the ventricles of the larynx oval recesses communicating by a transverse elliptical orifice with the interior of the larynx, and prolonged upward and outward as the laryngeal pouches. The upper edge of the ventricle, somewhat prominent through the presence of connective tissue, is known as the false vocal cord, since it is not concerned in the production of the voice, the lower edge corresponding with the upper border of the vocal membrane or true vocal cord, as it is often improperly called, and upon the vibration of which the production of the voice depends. From the ventricles the mucous membrane passes downward, lining the vocal membrane, cricoid cartilage, and finally becomes continuous with that of the trachea. The mucous membrane of the larynx is soft, thin, and pale red, its epithelium being of the ciliated columnar form, except upon the so-called vocal cords, where it is squamous like that of the

FIG. 515.



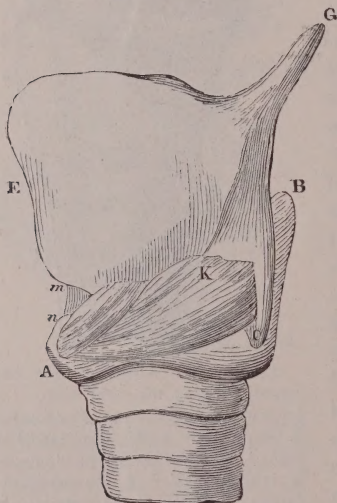
Longitudinal section of the human larynx, showing the vocal cords, 1, ventricle of the larynx; 2, superior vocal cord; 3, inferior vocal cord; 4, arytenoid cartilage; 5, section of the arytenoid muscle; 6, 6, inferior portion of the cavity of the larynx; 7, section of the posterior portion of the cricoid cartilage; 8, section of the anterior portion of the cricoid cartilage; 9, superior border of the cricoid cartilage; 10, section of the thyroid cartilage; 11, 11, superior portion of the cavity of the larynx; 12, 13, arytenoid gland; 14, 16, epiglottis; 15, 17, adipose tissue; 18, section of the hyoid bone; 19, 19, 20, trachea. (SAPPEY.)



pharynx and mouth. While adhering tightly to the epiglottis, the vocal membrane, and the interior of the cricoid cartilage, the mucous membrane in other parts of the larynx is loosely attached to the subjacent parts by connective tissue.

The vocal membrane (Fig. 516), about seven lines long in the male and five in the female, bounding the anterior thirds of the aperture of the glottis, and consisting of elastic tissue, may be regarded as extending from the front and sides of the upper border of the cricoid cartilage, upward to the bases of the arytenoid cartilages, and to the lower part of the entering angle of the thyroid. The lower portion of each vocal membrane is the strongest, and may be seen at the front of the larynx in the interval between the thyroid and cricoid cartilages. The lateral portions are thin and are separated by the thyroid and arytenoid muscles from the alæ or wings of the thyroid. The upper margins of the vocal membranes—that is, the parts corresponding in position to the lower edges of the ventricles, extending on either side from the anterior prominent angle of the base of the arytenoid cartilages to the entering angle of the thyroid, being somewhat thickened, are usually described as the

FIG. 516.



External and sectional views of the larynx. A *n* B. The cricoid cartilage. E C G. The thyroid cartilage. G. Its upper horn. C. Its lower horn, where it is articulated with the cricoid. F. The arytenoid cartilage. E F. The vocal ligament. A K. Cricothyroid muscle. F *m*. Thyroid-arytenoid muscle. X *a*. Crico-arytenoid lateral. *a*. Transverse section of arytenoid transversus. *m n*. Space between thyroid and cricoid. B L. Projection of axis of articulation of arytenoid with cricoid. (CARPENTER.)

FIG. 517.

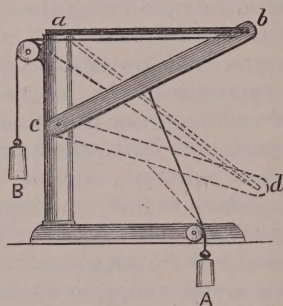


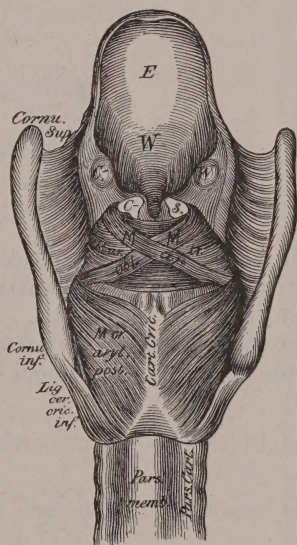
Diagram of a model illustrating the action of the levers and muscles of the larynx. The stand and vertical pillar represent the cricoid and arytenoid cartilages, while the rod *b c*, moving on a pivot at *c*, takes the place of the thyroid cartilage; *a b* is an elastic band representing the vocal ligament. Parallel with this runs a cord fastened at one end to the rod *b c*, and, at the other, passing over a pulley to weight B. This represents the thyro-arytenoid muscle. A cord attached to the middle of *b c*, and passing over a second pulley to the weight A, represents the crico-thyroid muscle. It is obvious that when the bar *b c* is pulled down to the position *c d*, the elastic band *a b* is put on the stretch. (HUXLEY.)

“true vocal cords,” as contrasted with the false vocal cords, or the upper edges of the ventricle. As a matter of fact, however, apart from the vocal membrane, of which they are the upper thickened edges, no such

organs as vocal cords exist, either structurally or functionally. That the whole vocal membrane consists of elastic tissue is readily shown by the yellowish color of the tissue being distinctly seen through the overlying mucous membrane, which in this situation is quite thin. The essentially membranous character of the vibrating portion of the larynx is well seen in the case of the elephant, in which animal the vocal membranes are two elastic bands almost two inches in length and nearly three-quarters of an inch in breadth. Inasmuch as the vocal membranes extend from the arytenoid cartilages to the thyroid, it is evident that if these cartilages approach or recede from each other the vocal membranes will be relaxed or tensed accordingly, and that if the arytenoid cartilages be rotated backward or forward the vocal membranes will recede or diverge from each other, or will approach and become parallel. Such changes in the tension of the vocal membranes and in the form of the glottis, just referred to, are, as a matter of fact, brought about through the action of the intrinsic assisted by the extrinsic muscles of the larynx upon the thyroid and arytenoid cartilages.

Thus the crico-thyroid muscle (Figs. 516, 517) arising from the front and side of the cricoid cartilage to be inserted in the lower border of the thyroid in drawing the latter downward and forward, and therefore away from the arytenoid, tenses the vocal membrane. On the other hand the thyro-arytenoid muscle (Figs. 514, 517) arising from the inner surface of the thyroid cartilage to be inserted into the outer surface and base of the arytenoid cartilage, in drawing the latter forward relaxes the vocal membrane. The effect of the contraction of the crico-thyroid muscles in stretching the vocal membranes is increased by the simultaneous contracting of the arytenoid, crico-thyroid, postici, and sterno-thyroid muscles, that of the thyro-arytenoid in relaxing the vocal membranes by the action of the crico-thyroid lateralis and thyrohyoid muscles. The posterior crico-arytenoid muscle (Fig. 518), so called

FIG. 518.



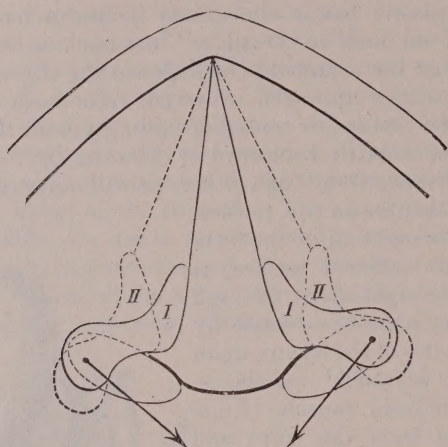
Larynx from behind with its muscles; *E*, Epiglottis, with the cushion *W*; *C*, (*W*) Cartil. Wrisbergii; *C. S.* Cartil. santoriniana; *C. c.* Cartil. cricoidea. Cornu sup. cornu inf. cartilaginis thyroideae; *M. ar. ir.*, Musculus arytenoideus transversus; *Mm. ar. obl.*, Musculi arytenoidei obliqui; *M. cr. aryl. post.* Musculus crico-arytenoideus posticus; *Pars. cart.*, Pars cartilaginea; *Pars memb.*, pars membranacea trachæ. (LANDOIS.)

on account of its arising from the posterior surface of the cricoid cartilages to be inserted into the external angle of the base of the arytenoid cartilage, in rotating the latter backward not only widens the glottis (Fig. 519), but, as just mentioned, also assists in tensing the vocal membrane. The lateral crico-arytenoid muscles (Fig. 520) lying under the wing of the thyroid cartilage, arising from the upper lateral border



of the cricoid to be inserted into the external angle of the base of the arytenoid cartilage, in contracting rotate the latter forward and press together their inner edges, and not only narrow the glottis but assist in relaxing the vocal membrane. The arytenoid muscle, consisting of

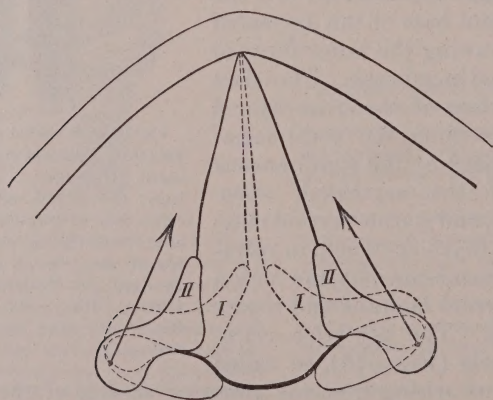
FIG. 519.



Lozenge shape of the glottis, produced by the action of the posterior crico-arytenoid muscle. (Kuss.)

transverse and oblique fasciculi, being attached to the posterior concave surface of the arytenoid cartilages, in contracting draw the latter together and so narrow the glottis. In addition to the muscles just described, there are usually found a few muscular fibres passing from the epiglottis to the thyroid and arytenoid cartilages, known as the thyro- and aryteno-

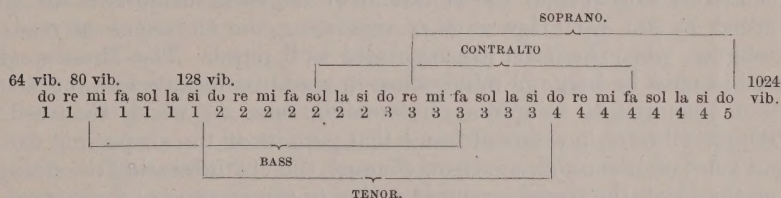
FIG. 520.



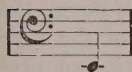
To illustrate action of crico-arytenoid lateralis muscle. (Kuss.)

epiglottidean muscles, whose functions appear to be to depress the epiglottis and compress the laryngeal pouches respectively. Such being, in brief, the general structure of the larynx, it follows, from what was

said in the preceding chapter, that if the air expired from the lungs and ascending in the trachea in passing through the glottis throws the elastic vocal membranes into vibration, a sound, the voice, will be produced, the character of which will depend upon the tension of the vocal membranes, shape of the glottis, etc., just as we can produce a sound by forcing air by means of a bellows through a glass tube over the mouth of which have been stretched two elastic membranes. Lest, however, the analogy of the bellows and pipe to the lungs and trachea might suggest the idea of the larynx acting as an organ pipe, or that the misnomer vocal cords might give the impression that the larynx acts as a stringed instrument, let us compare the range of the voice, on the one hand, with that of notes as produced by organ pipes and strings on the other, and it will then become evident that the larynx does not act like either. The range of the human voice in the two sexes, and of the bass and tenor voice in the male and female, can be most conveniently illustrated by musical notation after Müller,<sup>1</sup> as follows:

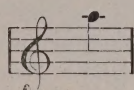


from which it will be seen that the voice ranges ordinarily from  $mi_1$



80 vibrations per second, the lowest note of the male bass

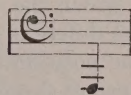
voice, to  $do_5$   $Ut_5$



1024 vibrations per second, the highest

note of the female soprano or tenor, though it should be mentioned that

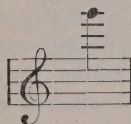
some bass voices reach the  $fa_1$



42.6 vibrations per second

of the octave below the above scale or even lower, and some soprano

voices the  $sol_5$



1536 vibrations per second above and

even higher. The human larynx being capable, therefore, in the case of a man of emitting ordinarily a note due to 80 vibrations a second, and in a woman of one due to 1024 vibrations, would have to be over five feet long and six inches long, respectively, if it acted like an organ

<sup>1</sup> Physiology, trans. by Baly, vol. ii. p. 1030. London, 1842.



pipe, since that would be the length of the pipes giving those notes, the notes of an eight foot pipe and six inch pipe being due to 64 and 10.24 vibrations a second, respectively. Similarly no notes as deep as those of the bass voice can be produced by strings as short as the vocal membranes, however the latter may be relaxed.

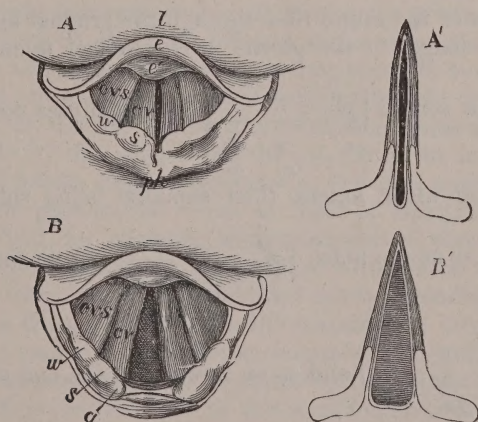
Further apart from the fact of the vocal membranes being too short to produce bass notes on the supposition that they act like strings, the E string of the double bass for example, vibrating  $41\frac{1}{4}$  times per second, the ratio of the vibrations of the vocal membranes to the weights extending them is not the same. Thus, for example, while it is well known that the vibrations of a string are doubled by quadrupling the extending weights, the number of vibrations being proportional to the square root of the weight, the vibrations of the vocal membranes, as shown experimentally by Müller,<sup>1</sup> are not so doubled by quadrupling the extending weight, the vibrations not reaching the octave above, as in the case of a string, by several semitones. On the other hand, it has been shown by Müller that the vibrations of the vocal membranes are governed by the same law as that regulating the vibrations of reeds or tongues, when the latter are associated with pipes. The latter qualification must be borne in mind, since in reed instruments like the accordion, concertina, seraphine, harmonium, etc., in which the reed or tongue vibrates in a sort of frame that permits of the air passing out on all sides of it through a narrow channel, thereby increasing the strength of the blast, the sound produced is due to the vibration of the reed or tongue alone, and is regulated entirely by the length and elasticity of the latter. In reed instruments like the clarinet, bassoon, and oboe, however, in which the single or double reeds are associated with pipes, the air setting the reed in vibration traverses the whole length of the pipe before escaping into the atmosphere, and consequently the sound produced is due to the vibrations of both reed and pipe combined, and not to either of them singly—the two sounds accommodating themselves to each other in such a way that only one sound is heard, the fundamental being neither always that of the reed alone nor of the pipe alone. In the case of the clarinet, in which the reed is a single broad tongue, and in the oboe and bassoon, in which the reeds are double and somewhat spoon- or spatula-shaped, the different notes are produced by closing or opening a series of holes, the position of which has been determined by experiment. In the reed pipes of the organ, however, in which the reed is inserted into the pipe through a plug, each note has a separate pipe. It was established more especially by Weber<sup>2</sup> that reeds associated with pipes, as in the case of the voice and of the instruments just mentioned, possess certain well-marked properties by which they can be at once distinguished from other musical instruments, such as organ pipes, flutes, etc., and with which, in the case of the voice, they may be confounded. Among the most important of such properties may be mentioned, 1st, that the pitch of a reed, though it cannot be raised, may be lowered by joining it to a tube; but at the utmost by not more than an octave; 2d, that the fundamental note of the reed so lowered may be raised

<sup>1</sup> Op. cit., p. 985.

<sup>2</sup> Poggendorf: *Annalen*, xvi. xvii.

again to its original pitch by a lengthening of the tube, the latter then yielding the same fundamental note as the reed of the instrument without the tube, whilst by a further lengthening the pitch is again lowered, and by a still further lengthening raised again, 3d, that the length of the tube necessary to lower the note to any given pitch, depends on the relation existing between the rapidity of the vibrations of the tongue of the reed and those of the column of air in the tube, each taken separately. Accepting the above as the essential conditions which an instrument must fulfil in order to constitute a reed instrument, Müller<sup>1</sup> showed that the larynx, in fulfilling the same, must be regarded as a reed instrument, the vocal membranes being comparable to membranous vibrating tongues. The conclusion just arrived at, based upon acoustic principles, that the larynx is a reed instrument, is fully borne out, not only by the fact that in several instances persons rendered voiceless by the loss of their larynx, have been enabled to speak, so as to be perfectly heard through the introduction into the trachea of a tube containing a reed, but also by observing directly the larynx during phonation with the laryngoscope. Among the first to investigate the larynx in this way was Manuel Garcia,<sup>2</sup> so distinguished as a singing teacher, whose experiments were made principally with the view of determining the scientific principles upon which the teaching of singing should be based, and which, up to that time, had been taught by purely empirical methods. The difficulty of observing the vocal membranes during phonation on account of the epiglottis hiding so much of their anterior portions, especially in the production of high notes, is a familiar fact to

FIG. 521.



A, the glottis during the emission of a high note in singing. B, an easy or quiet inhalation of air.

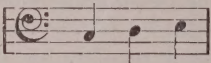
those in the habit of using the laryngoscope. The perfect control, however, possessed by Garcia over his own vocal organs, together with the skill with which he examined them in his own person, enabled him finally to determine very satisfactorily the changes actually undergone

<sup>1</sup> Op. cit., pp. 985, 999, 1023.

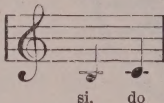
<sup>2</sup> Proc. of Royal Society Lond., 1856, vol. vii p 399.

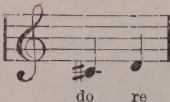


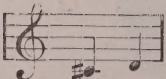
by the glottis and vocal membranes during singing, the accuracy of the observations, models of scientific research, being fully confirmed by later observers. The changes in the glottis during ordinary breathing (Fig. 521, A A') having been already described, it will be only necessary in this connection to recall the fact, that during inspiration the glottis, through the action of the crico-arytenoidei postici muscles, is widely dilated, and that during expiration, the larynx appearing to be passive, the air is gently forced out through the glottis by the expiratory movements of the chest. Garcia having first noticed the movements of the larynx during his ordinary breathing, observed next that just at the moment of making a vocal effort, his glottis underwent an entire change, the arytenoid cartilages being so approximated that the vocal cords were brought parallel to each other (the distance separating them, it may be here mentioned, not exceeding the one-twelfth of an inch), the glottis then appearing as a narrow slit (Fig. 521, B B'). The glottis being thus prepared, so to speak, for the emission of a note through the action of the expiratory muscles, air is forced through the slit or chink, the effect of which is that the vocal membranes are thrown into vibration, the particular note emitted being due essentially to the length and tension of the latter. Thus, according to Garcia, in the production of the bass

notes  the glottis is agitated by large and loose vibrations throughout its entire extent, the lips comprehending in their length the anterior apophyses of the arytenoid cartilages and the vocal cords.

As the pitch of the sound rises through the gradual apposition of the apophyses the length of the glottis is encroached upon, and with the

emission of the sounds  the apophyses touch each other throughout their whole extent, their summits being solidly fixed one

against the other at the notes  With the production of

the notes , and so on upward to the end of the register,

the vibrations are due to the vocal membranes alone, the length of the glottis diminishing, and the cavity of the larynx becoming very small as the pitch of the voice continues rising. These changes undergone by the glottis in the shape and size and in the length and tension of the vocal membranes in the production of low and high notes by the larynx, as observed by Garcia and subsequent investigators, become intelligible when it is remembered, as shown in the last chapter, that the pitch of

the note—that is, the number of vibrations per second—rises as the length of the string, pipe, or membrane diminishes, or the tension increases, the change in the shape of the glottis and of the tension of the vocal membranes being accomplished by the action of the muscles, as already explained. Thus, men have deeper voices than boys and women, their larynx being larger, and their vocal membranes longer. That the aperture of the glottis is narrowed during the production of sounds any one can convince himself by comparing the time of an ordinary expiration with that required for the passage of the same quantity of air during a vocal effort, and that the size of the aperture varies with the pitch of the note, from the fact of there being a far less passage of air during the production of a low note than in that of a high one. That the production of low and high notes is due to variations in the tension of the vocal membranes, as brought about by the action of the thyro-arytenoid and crico-thyroid muscles, is made evident during the passage of the voice from one extreme of the scale to the other by the movement of the thyroid on the cricoid cartilage, which is quite apparent if the tip of the finger be placed over the crico-thyroid ligament. As illustrating the nicety and precision with which the tension of the vocal membranes is regulated by muscular contraction, let us suppose, with Müller,<sup>1</sup> that the average length of the vocal membrane in man during repose is about  $\frac{7.3}{100}$ th of an inch, and during the greatest tension  $\frac{9.3}{100}$ th, the difference being, therefore,  $\frac{2.0}{100}$ th, or the  $\frac{1}{5}$ th of an inch, and that in the female the corresponding extremes are about  $\frac{5.1}{100}$ th and  $\frac{6.3}{100}$ th, the difference being  $\frac{1.2}{100}$ th, or the  $\frac{1}{8}$ th of an inch, and that the natural compass of the voice is about two octaves, or twenty-four semitones. Such being the case, as any cultivated voice can sing ten intervals between the twenty-four semitones, such a voice can produce 240 sounds, necessitating, however, over 240 different states of tension. Inasmuch, however, as the available length of vocal membrane to be tensed is only the  $\frac{1}{5}$ th and the  $\frac{1}{8}$ th of an inch in the sexes, it follows that in the production of each of the 240 sounds the vocal membrane must be diminished voluntarily by the  $\frac{1}{1200}$ th and the  $\frac{1}{1920}$ th of an inch in the case of the male and female singer, respectively, and by considerably less in the case of such phenomenal voices as those of Bastardella, Catalani, Cruvelli, and Patti, for example, with a compass of three octaves, and even more. The remarkable distinctness with which certain voices could be heard, like those of the celebrated basso, Lablache, and the late Madame Parepa Rosa, clearly above the sounds of a large chorus and orchestra, is due rather to the absolute accuracy with which the tension of the vocal membranes could be regulated by those great singers, to the purity of their tones rather than to the mere loudness or intensity. It should be mentioned, however, that the singers just referred to were of magnificent physique, as might have been expected, the power of the voice being due to the force with which the air is expelled from the lungs. As the action of the diaphragm and abdominal muscles has already been considered, it will be only necessary in this connection to recall what has already been said, that the inspiratory and expiratory acts can be



so nicely balanced by a skilful singer as to enable him to produce the most delicate tones. It need hardly be added that while sounds may be uttered, and even words spoken during inspiration, that the true and natural voice, and, as we shall see presently, articulate speech are only produced during expiration. While, in childhood, the general character of the voice is the same in both sexes, in the adult condition the male voice differs very much from that of the female, the difference becoming marked at the age of puberty. If castration be performed, therefore, the contralto, or soprano, voice of the boy will be retained through life, and such a voice being susceptible of considerable cultivation advantage was cruelly taken of the fact at one time to fill choirs with desirable voices. After the age of puberty, however, the quality of the female voice remains the same, except in gaining strength and extending its compass. At this period, in the case of the male, however, the whole character of the voice changes through the development of the larynx. While the intensity of the voice in both sexes depends upon the force with which the air is expelled through the larynx, and the range or pitch, bass, tenor, contralto, and soprano, upon the length and tension of the vocal membranes, the quality of any particular individual voice, male or female, depends upon the shape, size, and general make of the larynx, and on the character of the auxiliary resonating cavities. In concluding our account of the production of the voice, a brief description, at least, of the influence exerted by the accessory vocal organs, viz., the trachea, ventricles, superior vocal cords, epiglottis, pharynx, nasal cavities, and mouth, should be offered. The trachea not only serves to conduct air to the larynx, but through the vibration of its own column of air reinforces the sound produced by the larynx, the vibration being perfectly appreciable if the finger be placed upon the trachea during a powerful vocal effort. The ventricles probably, also, intensify the sound, the homologous parts being enormously developed in monkeys and apes possessing very loud voices, such as the South American howler (*Mycetes*), the chimpanzee, and gorilla.

That the superior or false vocal cords and the epiglottis are not essential to the production of the voice, can be shown by experiments like those of Longet,<sup>1</sup> in which the above parts were removed in animals without the voice being materially affected, and in man those cases in which the epiglottis had been lost through wounds or disease. The pharynx, mouth, and nasal fossæ, acting as resonating cavities, modify, however, very considerably the sounds produced by the vocal membranes. Indeed, in the production of the natural voice their resonance is essential. Thus, while in the production of low notes the velum palati is fixed, and the bucco-pharyngeal and naso-pharyngeal cavities reinforce the laryngeal sounds, in the passage upward to the higher notes these cavities are reduced in size, the isthmus contracting until, with the emission of the highest notes, the nasal fossæ is shut off entirely, and the mouth and pharynx alone resound, the tongue at the same time being drawn back into the mouth with its base projecting upward and

<sup>1</sup> *Physiologie*, tome ii. p. 728. Paris, 1869.

the tip downward, the capacity of the resounding cavity is still further diminished. Such being the mechanism by which the chest tones or chest register are produced, it is only necessary to add, that if the velum palati be thrown forward instead of backward, thereby cutting off the mouth from the pharynx, the resonance being then due to the nasopharyngeal cavity, that we pass from the chest register into that of the head tones or head register.<sup>1</sup> According to the late Madame Seiler,<sup>2</sup> however, the head tones are due to the vocal membranes being firmly approximated posteriorly, an oval opening being left with vibrating edges involving only one-half or one-third of the vocal membranes, which gradually contracts as the pitch of the tone rises. As in the case of the head register, so in that of the falsetto or middle register of the female, a difference of opinion still prevails as to the exact manner of its production. Thus, while, according to Fournié,<sup>3</sup> the falsetto is due to the tongue being pressed strongly backward and the epiglottis forced over the larynx; according to Seiler,<sup>4</sup> it is due to the thin, fine edges of the vocal membranes alone vibrating. While the distinction between the chest, falsetto, and head registers so far as pitch is concerned, is not an absolute one, and while we find that every voice possesses all three registers, nevertheless the chest register almost characterizes male voices and the contralto of the female, the falsetto being the most natural voice of the soprano, though the latter voice is capable of chest tones, while the head voice is particularly well developed in tenors and in the female voice. The falsetto is but little cultivated at the present day by tenors, and even when it or either of the other two registers is particularly well developed the singer should endeavor to pass as insensibly as possible from one register to another, to give the impression that his voice possessed but one.

## SPEECH.

While the position of man as the head of the animal kindom depends upon the development of his intelligence, there can be no question that his superiority over all other animals is, to a great extent, due to his being able to convey his ideas to others by expression, or articulate speech. Speech is voice modulated by the throat, nose, tongue, and lips. Voice may, therefore, exist without speech, and if the production of the voice be restricted to the vibrations of the vocal membranes, it may be said that speech can exist without voice, since, in whispering, the vibrations of the muscular walls of the lips replace those of the vocal membranes, a whisper being, in fact, a very low whistle. Articulate sounds are usually divided by orthepists into vowels and consonants: vowels being continuous sounds due to the voice alone, but modified by the form of the aperture through which they pass out; consonants, interrupted sounds due to the interruption, more or less, of the voice, and sounded with vowels. This classification is not, however, a very natural one, since the sound of the English *i*, being a diphthongal sound, cannot be prolonged like a true

<sup>1</sup> Fournié : *Physiologie de la voix et de la parole*, p. 421. Paris, 1866.

<sup>2</sup> *The Voice in Singing*, p. 56. Phila., 1868.

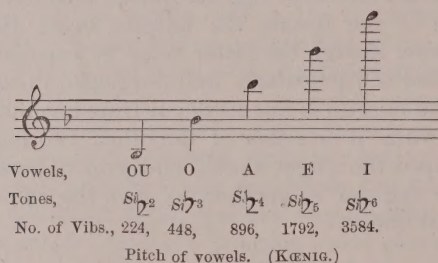
<sup>3</sup> *Op. cit.*, p. 463.

<sup>4</sup> *Op. cit.*, p. 56.



vowel (a, o), while certain consonants (l, r, f) can be pronounced without the current of air being interrupted. The vowel sounds, by which we mean u, o, a, e, are due to the reinforcing of the overtones of the fundamental tone of the larynx by the cavity of the mouth, the changes in the shape of which give rise to so many resonantors, each of which is adapted to the reinforcing of the particular overtone to which, together with the fundamental tone, the particular vowel is due. The presence of overtones coexisting with the fundamental tone of the larynx in the emission of vowel sounds, and the determination of what particular overtone accompanies the fundamental tone in the production of any particular vowel, can be shown by the Kœnig manometric apparatus described in the last chapter. Thus the vowel sound u is due to the fundamental tone being emitted strong, the cavity of the mouth being made as deep as possible, by keeping the tongue down at the bottom, and pushing the lips out, the mouth then reinforcing the fundamental tone of the larynx, and tuned, according to Kœnig<sup>1</sup> and the experiments of the author, to the pitch of the note  $Si\frac{1}{2}_2$  (Fig. 522), due to 224 vibrations per second. The sound o is due to the

FIG. 522.



fundamental note of the larynx being present, but especially its first octave above being emitted also, and very strong, the cavity of the mouth being enlarged through the retraction of the lips so as to reinforce the octave, and tuned to the pitch of the note  $Si\frac{1}{2}_3$ , due to 448 vibrations per second. The sound a, like the preceding two vowels, is due to the presence of the fundamental tone of the larynx, but differs from o in that the fundamental is accompanied by the double octave above, the orifice of the mouth being so widened that the cavity of the mouth is tuned to the pitch of the note  $Si\frac{1}{2}_4$  due to 896 vibrations per second. In the production of the sound e the cavity of the mouth is still more retracted, reinforcing the third octave above the fundamental, the cavity of the mouth being tuned to the pitch of the note  $Si\frac{1}{2}_5$  due to 1792 vibrations per second. As the four vowels u, o, a, e, can be produced during one continuous expiration, during which the fundamental and overtones generated by the vocal membranes remain the same, by simply changing the shape of the mouth, it is evident that the production of each individual vowel will depend, as already mentioned, upon

<sup>1</sup> Quelques: Experiences d'Aoustique, p. 65. Paris, 1882.

which particular octave or overtone is reinforced by the cavity of the mouth, the pitch of the latter depending upon its shape, and that the shape of the mouth remaining unchanged, the corresponding vowel will be emitted as long as the expiration blast lasts. Now while the vowel *i* agrees with the four vowels just mentioned in being due to the reinforcement of an overtone, the fourth octave accompanying the fundamental by the cavity of the mouth, which in this instance is tuned to the pitch of the note  $S_{126}$ , due to 3584 vibrations per second, an octave higher than in the case of the vowel *e*, it differs from the true vowels in that, the cavity of the mouth remaining the same, if the expiratory blast be prolonged, it does not remain *i*, but becomes *e*. The vowels are the only real vocal sounds, it being only on a vowel that a note can be said or sung. Speech, however, is made up not only of vowels, but of consonants—that is, of sounds that are sounded in conjunction with a vowel. While the distinction between vowels and consonants, as already mentioned, is not an absolute one, it may be said that while vowels are due to the vibrations of the vocal membranes being modified by the mouth, consonants are due to the expiratory blast being interrupted in various ways in its course through the throat and mouth; the vibrations of the vocal membranes, when essential, being rather secondary in character. Consonants may be divided according to their manner of production, into two kinds, explosive and continuous, the sound of the explosive consonants being due to the sudden establishment or removal of a particular interruption, that of the continuous consonant to the air rushing continuously through some constriction, for example, explosive consonants are the labials *p*, *b*, dentals *t*, *d*, and gutturals *k*, *g*, *p*, *t*, and *k*, being uttered without the voice, *b*, *d*, and *g* (hard) with the voice—that is, are accompanied by a vowel sound. In uttering *p*, the lips are first closed, then the expiratory blast suddenly opening them, the sound is produced. Similarly the sudden interruption of the contact of the tip of the tongue with the hard palate, and of the root of the tongue with the soft palate gives rise respectively to the sounds *t* and *k*. The continuous consonants are subdivided into aspirates, resonants, and vibratory.

The aspirates include the labials *f*, *v*, the dentals *s*, *l*, *sh*, *th* (hard), *z*, *zh*, *th* (soft), and the gutturals *ch*, *gh*. Like the explosive consonants, some of the aspirates are uttered without the voice, as *f*, *s*, *l*, *sh*, *c*, *h*; some with the voice, as *v*, *z*, *zh*, *th*, *ch*. The resonants include the sounds *m*, *n*, *ng*, and the vibratory the sound *r*, common and guttural. Of the aspirates, *f* and *s* are formed through the lips and teeth being brought nearly in contact respectively; *th* through the placing of the tongue between the two partially open rows of teeth; *l* when the tip of the tongue is placed against the hard palate, and the air escapes at the sides; *sh* through the dorsal surface of the tongue being raised toward the palati, the passage-way between the two being thereby narrowed; *ch* and *gh* through the approximation of the root of the tongue to the soft palate. In the production of all of the resonants the vocal membranes vibrate and the nasal chambers resonate, the closing of the lips in particular giving rise to *m*, the contact of the tongue with the hard palate to *n*, and the approximation of the root of



the tongue to the soft palate to ng. The vibratory consonants include the various forms of the sound r, so called on account of being produced by the vibration of the constricted portion of the vocal passage; thus, the common r is due to the vibrations of the point of the tongue elevated against the hard palate; the guttural r to vibrations of the uvula or other parts of the walls of the pharynx. The tongue, while an organ of speech, is not essential, since after its loss the faculty of speech more or less perfect remains. Finally, while the consonant e is a breathed aspirate, it differs from all other letters in being formed in the larynx itself, the glottis being narrowed enough to produce a wind-rush, but not sufficiently to throw the vocal membranes into vibration. c is redundant, producing the same effect as k or s; q is equivalent to l, being used only before the vowel u; x is the same as ks at the end of a syllable, and z when beginning a word.

While the limits of this work will not permit of any further detailed consideration of orthœpy, or of any theory of the origin and growth of language in general, or of that of the language in which this work is written in particular, the above description will suffice as a general account of the production of articulate speech, a factor almost as important as that of intelligence in the development of civilization.

## CHAPTER LIII.

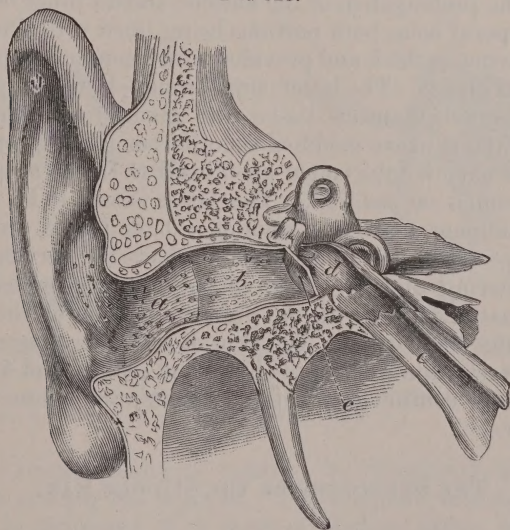
### THE STRUCTURE OF THE EAR, AND THE SENSATION OF HEARING.

THE organ of hearing is usually described as consisting of three parts, an external, middle, and internal ear, the latter including the auditory nerve. For convenience, as well as to avoid repetition, the functions of the three parts of the ear will be considered at the same time as that of the description of their structure.

#### THE STRUCTURE AND FUNCTIONS OF THE EXTERNAL EAR.

The pinna, auricle, or ear, in the ordinary sense of the term—that is, the portion projecting from the head (Fig. 523), with the exception of the

FIG 523.



View of parts composing the organ of hearing of the right side. *a.* Pinna and lobe. *b.* Meatus externus. *c.* Membrana tympani. *d.* Cavity of tympanum. *e.* Eustachian tube.

lower lobular portion consists of fibro-cartilage and presents certain prominences, the tragus and antitragus, ridges the helix and antihelix, which together with their fossæ, adapt it to receive the ærial vibrations giving rise when transmitted to the auditory nerve to the sensation of sound. Owing to the immobility of the ear, through the imperfect development



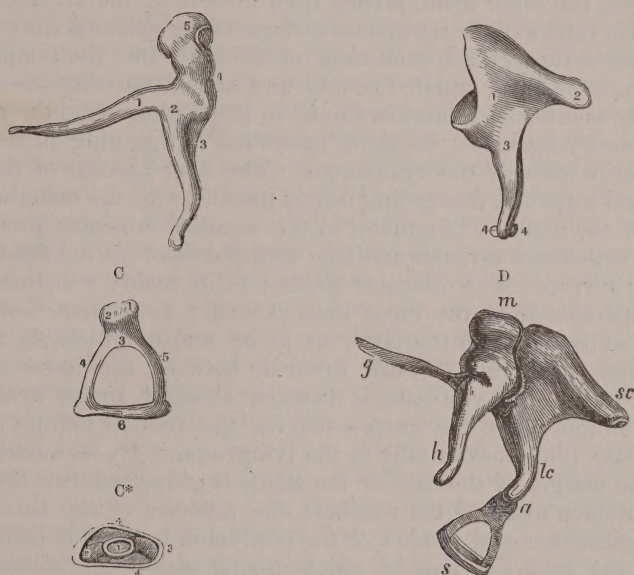
of the attolens, attrahens, and retrahens auri, as well as its intrinsic muscles, the external ear is not as functionally important in man as in the case of the lower animals for the appreciation of the intensity of sound, since persons deprived of it do not experience any sensible change in their power of hearing. That the external ear is, however, of use in enabling us to judge as to the direction of sounds, any one can convince himself by filling the convolutions with wax, or flattening the ear forcibly against the side of the head, when it will be found impossible to determine the direction from which the sound comes. Such is also the experience of those persons who have lost the external ear from wounds, etc. Indeed, there can be little doubt that we judge as to the origin and direction of sounds from the fact that the sound waves do not impinge upon the ears alike, and that the intensity of the sound is modified by the manner in which it falls upon the external ear and is reflected from it. Hence, in determining whether a sound proceeds from directly behind or in front of us, we usually incline the head in the direction from which we suppose it to come. The aerial vibrations having been collected by the external ear, are thence transmitted by the external auditory meatus from the concha or the deep concavity within the position of the antihelix and subdivided by the helix to the tympanum. The external auditory meatus, about an inch and a quarter in length, is directed inward and forward, upward and downward, and is narrowest at its middle portion. It consists of two portions, an interfibro-cartilaginous one, the prolongation of the auricle, and an inner osseous one, a part of the temporal bone, both portions being lined with skin. The skin of the outer portion is thick and provided with numerous hairs, sebaceous and ceruminous glands. The latter, small, round, brownish-yellow bodies imbedded in the subcutaneous tissue, and giving rise to the punctured appearance of the skin are modified sudoriferous glands, consisting, like the latter, of a narrow tube coiled upon itself in the form of a ball, and secrete the cerumen or ear-wax. The latter is said to be composed of fatty and albuminous matters of salts of soda and lime, and has a very bitter taste, a property which has been considered of service in preventing insects entering the ear. The cerumen, which probably consists of sebaceous matter mixed with the proper secretion of the ceruminous glands, lubricates the meatus. The skin of the inner osseous portion of the meatus is very thin, destitute of hairs and glands, and at the bottom of the meatus is continued over the tympanic membrane as its outer investing layer.

#### THE STRUCTURE OF THE MIDDLE EAR.

The middle ear, separated from the external ear by the tympanic membrane, includes the tympanum or drum of the ear, the ear bones, with their ligaments, muscles, the mastoid sinuses, and the Eustachian tube. The tympanum, an irregular cavity in the interior of the petrous portion of the temporal bone, is about half an inch in height and breadth, and perhaps the sixth of an inch from without inward, is closed in front by the tympanic membrane, at the back by the wall of the labyrinth,

and opens above and posteriorly into the sinuses and in front into the Eustachian tube. The tympanic membrane separating, as already mentioned, the external auditory meatus from the tympanum, is about two-fifths of an inch in height and breadth, somewhat funnel-shaped in form, and is disposed obliquely (Fig. 523, *c*), its outer depressed surface or umbo being directed downward and forward. The tympanic membrane is inserted by the greater part of its circumference into a groove which, while in the adult is regarded as a portion of the temporal bone, is in reality the only part visible of an originally entirely separate osseous ring, the homologue of the tympanic bone of the lower vertebrates, but which in man, instead of remaining distinct as in them, coössifies as development advances with the temporal bone, and grows outwardly as

A FIG. 524. B



Bones of the tympanum of the left side. A. Malleus: 1, long or slender process; 3, the handle; 4, short process; 5, head. B. Incus: 1, body; 2, short or posterior process; 3, the long process with the orbicular process 4. C. Stapes: 1, head; 4, 5, crura; 6, base. D. The three bones in their natural connection: *m*, malleus; *sc*, incus; *s*, stapes. C\*. Base of the stapes.

the osseous external auditory meatus, its morphological significance being thereby entirely lost sight of. The tympanic membrane, thin and translucent, is composed of a layer of fibrous tissue, the *membrana propria*, covered externally by the skin of the external auditory meatus, and internally by the mucous membrane of the tympanum, the latter being continuous with that lining the Eustachian tube. The fibrous layer of the tympanum consists of two sets of fibres, of which the greater part radiate from its centre, the remaining ones being concentrically disposed at the periphery. The little ear bones (Fig. 524), three in number, the malleus, incus, and stapes, are disposed within the tym-



panum from before backward in the order named. The malleus, so called on account of its resemblance to a hammer, is suspended vertically from the floor of the tympanum by a slender band of fibres, the suspensory ligament, which passes into its head, the latter articulates through an oval facet covered with cartilage with the body of the incus. The malleus is also connected with the tympanic membrane, its tapering slightly twisted manubrium or handle passing down into the fibrous layer of the latter as far as its centre. From the neck of the malleus, or the constricted portion below the head, two processes are given off, one of which, the largest, or *processus gracilis*, projecting at right angles, passes into the Gasserian fissure to be attached to the *laxator tympani* muscle arising from the spinous process of the sphenoid bone, and so called on account of its relaxing the tympanic membrane. The tensor muscle tensing the tympanic membrane and inserted into the neck of the malleus, on the other hand, arising from the end of the cartilage of the Eustachian tube, and the contiguous surfaces of the sphenoid and temporal bones, passes through a special canal of the latter into the tympanum.

The incus or anvil, situated behind and articulated with the malleus as already mentioned, is also sustained in its position by a fibrous band, its suspensory ligament, its short backwardly projecting process with the posterior part of the tympanum. The long process of the incus curved and tapering, descending nearly parallel with the manubrium or handle of the malleus, terminates in the so-called orbicular process, by which it articulates through cartilage with the facet on the head of the stapes or stirrup. The orbicular process is in reality a distinct bone, being separable from the incus even at birth; soon after, however, it becomes so ossified with the latter as to be undistinguishable from it. The stapes or stirrup, situated inwardly between the incus and the foramen ovale of the vestibule, is disposed at right angles to the long process of the incus, the *crura*—that is, the portion joining its head and its base, lying horizontally in the tympanum. By its annular ligament, the margin of the base of the stapes is connected with the border of the foramen ovale of the vestibule, the pressure of the base of the stapes against the oval window or the perilymph back of it being regulated by the *stapedius* muscle, which arising within the hollow of the pyramid, or the conical eminence projecting from the back part of the tympanum, is inserted into the head of the stirrup. The mastoid sinuses, so called from being situated in the interior of the mastoid portion of the temporal bone, are irregular cavities lined with mucous membrane, which communicate by a large orifice with the upper and back part of the tympanum. The Eustachian tube (Fig. 523, *e*) about an inch and a half long and somewhat trumpet-shaped in form, extends from the front part of the tympanum obliquely downward, forward, and inward, terminating by an oval orifice in the pharynx on a level with the turbinated bone at the back of the posterior nasal orifice. The Eustachian tube consists of two portions, an upper osseous portion situated in the petrous portion of the temporal bone and opening into the tympanum, and a lower fibro-cartilaginous portion opening into the pharynx, the two portions being united within the angle between the squamous and petrous portions of the temporal bone. It is lined with

mucous membrane provided with ciliated epithelium, continuous on the one hand with that of the tympanum, and on the other with that of the pharynx. The existence of such a tube as that just described, putting the cavities of the middle ear in communication with that of the pharynx, as well as the presence of a chain of bones connecting the membrana tympani with the oval window of the vestibule, will become intelligible when the development of the ear is considered.

### FUNCTIONS OF THE MIDDLE EAR.

Such being in general the structure and relations of the tympanic membrane, ear bones, Eustachian tube, etc., if the aërial vibrations collected and transmitted by the auricle to the external auditory meatus throw the tympanic membrane into vibration, the vibrations of the latter will in turn be transmitted by the ear bones through the intermediation of the vestibule, etc., to the terminal filaments of the auditory nerve, and so give rise to the sensation of sound. The importance of the membrana tympani in audition is shown by the fact that the acuteness of hearing is always more or less affected in those cases in which the membrane is thickened, perforated, or destroyed, and that relief is obtained by the wearing of an artificial membrane if the latter can be tolerated. This becomes perfectly intelligible when it is remembered, as shown by Müller,<sup>1</sup> that while aërial vibrations are communicated to solid bodies like the ear bones only with difficulty and with considerable diminution in their intensity, they are communicated very readily to the same, a tense membrane like the tympanic membrane intervening, the fact of the membrane being fixed at the periphery, and having air on both sides of it being also most favorable conditions. That membranes of as small extent as that of the membrana tympani when stretched are readily thrown into vibration, can be shown by experiments like those of Savart<sup>2</sup> in which sand strewed over their surface was cast off, on sonorous vibrations being excited in their vicinity. It is a well-known fact, that membranes vibrate more powerfully, more intensely, when relaxed than when tensed, hence the sensitiveness to all sounds experienced in facial palsy, which is due to the want of innervation of the tensor tympanic muscle by the filaments of the paralyzed facial supplying it. It is also worthy of mention in this connection, that the vibrations of the membrana tympani are more intense in proportion as the latter approaches a vertical position, as accounting to some extent for the appreciation of sounds by musicians, in some of whom the tympanic membrane is almost vertically disposed, whereas in persons with but little ear for music, the membrane is very oblique in position. It has already been explained, that sounds not only differ in their loudness or intensity, but in their pitch or number of vibrations per second as well, and since we hear sounds of different pitch, it is obvious, therefore, that there must be some means of tuning—that is, of tightening or relaxing the tympanic membrane, so that the vibrations of the latter shall be the same per second as those to which

<sup>1</sup> Physiology, vol. ii. p. 1248.

<sup>2</sup> Journal de Physiologie, tome iv. p. 203. Paris, 1824.



the particular note or notes heard are due. That is to say, every sonorous aërial wave—that is, a condensation and a rarefaction,—bending the tympanic membrane once in and once out, the rate of vibration of the membrane must be the same as that of the vibration of the sonorous body causing it, if the particular sound due to the latter is to be heard. That the membrana tympani is relaxed for sounds of low pitch and tensed for those of high pitch, is shown by the insensibility to low tones, and marked appreciation to high ones, being proportional to the extent to which the membrane is tensed. Thus, if the mouth and nose being closed, we attempt to breathe forcibly by expanding the chest, the air within the tympanum becoming rarefied, the tympanic membrane will be forced in by the external air and rendered more tense, the effect of which is that, as Dr. Wollaston<sup>1</sup> showed, we become deaf to low sounds. A similar deafness to sounds of low pitch is also produced, the nose and mouth being stopped when a strong effort is made to expire, the increased tension of the membrane being due, however, in this instance to the air being forced into the tympanum through the Eustachian tube instead of being sucked out of it and the membrane being pushed outwardly. A sudden concussion may produce temporary deafness in either of the above ways—that is, by forcing air either into or out of the tympanum.

It is evident, from the facts just mentioned, that the function of the Eustachian tube is the maintaining of equilibrium between the air within the tympanum and the air without. Hence if the tube be closed, which is usually the case, according as the external air becomes denser, as in descending in a diving-glass, or, rarer, as in making high mountain ascents, the tympanic membrane will be pushed in or out in either case, will be rendered more tense and pain and deafness experienced, both of which can, however, be usually relieved by the act of swallowing, which, in opening the Eustachian tube, reëstablishes the equilibrium between the internal and external pressure. It may be mentioned, in this connection, that the Eustachian tube is opened by the contraction of the tensor palati, levator palati, and the palato-pharyngeus muscles; the tensor palati, in drawing the hook of the cartilage outward, and the levator palati, in drawing the end of the cartilage upward and inward, enlarge and widen its pharyngeal orifice, the palato-pharyngeus fixing the cartilage. With the relaxing of the muscles just mentioned, through the elasticity of the cartilage, the tube then closes again almost entirely, a narrow chink alone remaining. Since, while the Eustachian tube is open, the cavity of the tympanum is in communication with that of the pharynx, it follows that if we swallow several times in succession, the nose and mouth being closed, that the air will be gradually drawn from the tympanic cavity, the membrane being rendered tense by the external atmospheric pressure, as in the case just mentioned, in which forced inspiratory efforts were made, and an insensibility to low sounds experienced. That the tympanic membrane is tensed for high sounds is shown by the fact that in certain individuals,<sup>2</sup>

<sup>1</sup> Philos. Trans. Lond., 1820, p. 306.

<sup>2</sup> Blake: Trans. of the Amer. Otological Soc., vol. v. p. 77. Boston, 1872.

whose ordinary limit of appreciation was of sounds due to fifteen hundred vibrations per second by voluntary contraction of the tensor tympani muscle, this was increased, so that sounds could be heard due to 2500 vibrations per seconds. There can be little doubt, then, that the membrana tympani is relaxed or tensed, according as the sonorous vibrations are low or high in pitch, and that the variations in the tension of the membrane are regulated by the action of the laxator and tensor tympani muscles. While there is a great difference in individuals, as regards the appreciation of sounds, some persons being insensible to the hum of insects, the chirrup of the sparrow, the squeak of the bat; others to the high sounds of small organ-pipes, or even the highest notes of the piano; there is a limit, nevertheless, to audibility in all, the tympanic membrane failing to link together into a continuous tone vibrations succeeding each other less rapidly than 16 a second, or more so than 38,000 a second. In the former case, we are conscious only of separate shocks; in the latter, we are unconscious of sound altogether. The range of audibility lying within the above limits embraces, therefore, about 11 octaves; of which about two-thirds, or 7 octaves only, are, however, made use of in music. It is true, that we obtain from the lowest C of the piano the note due to 32 vibrations per second, and from the lowest A of the new grand piano are due to 27 vibrations per second, and from a closed organ-pipe 16 feet long, or an open one 32 feet long, the lowest C, due to 16 vibrations per second, but the latter sound, and that of the lowest C or A of the piano, are so unmusical, so dull and groaning in character, that they are but little used. The deepest tone made use of in orchestral music being that due to the E string of the double bass, giving  $41\frac{1}{4}$  vibrations, the highest that of the D of the piccolo flute, due to 4752 vibrations per seconds; it may be said that practically the range of musical sounds is confined between 40 and 4000 vibrations per second, the highest C of the piano reaching 4224 vibrations per second—that is, in round numbers, as just said, about 7 octaves. Even within such limits the immense number and kind of sonorous waves that fall upon the tympanic membrane while listening to a grand opera as given by the leading artists, together with full choral and grand orchestral accompaniment, must impress one with the remarkable acoustic properties of the membrana tympani, so small and delicate, and yet so susceptible to such an immense number and variety of sounds. But little imagination is required to picture to one's self, during the performance of an opera, the sonorous waves flowing across the auditorium, and breaking upon the drum of the ear like those of the ocean upon some weather-beaten rock or beach, the long waves, from 35 to 12 feet in length proceeding from the deep bass instruments and voices of the basses like billows from the distant sea, the short ones from 30.3 inches in length, like ripples or white caps, from the violins, flutes, and voices of the tenors and sopranos, with intermediate ones of different lengths, and yet all following each other in such orderly mathematical sequence that, amidst such a variety of sounds, we are conscious of nothing but melodious and harmonious tones. From the fact of our being able to appreciate the latter, it is obvious that the tympanic membrane is susceptible of being



impressed by simultaneous as well as by successive sounds, and while the limits of this work do not permit of any consideration of harmony, discord, of cords, of consonant intervals, or those that give the ear a sense of relief, or dissonant ones that must be resolved, etc., it seems proper to point out and illustrate the fact that the vibrations to which harmonious sounds are due are in a definite ratio to each other, and, that, whatever the cause may be, sounds are harmonious in proportion as the ratio between the number of the vibrations giving rise to them is a simple one.

The simplest ratio being one to one, two sounds, as produced by the siren, for example, will be in perfect union, if the pitch of both be the same. The next simplest ratio being 1 to 2, a harmonious sound will remain, if with the fundamental its first overtone above, or octave, be at the same time given—that is, if with  $Ut^3$   $C^3$  256 vibrations per second,  $Ut^4$ ,  $C^4$  512 vibrations per second be also sounded. The waves, never interfering with each other, will give rise to no discord, and the two sounds blended into one may be continued indefinitely. Proceeding in the same manner, according to the simplicity of the ratio, the next in order will be that of 2 to 3, or C to G—that is, with  $Ut^3$   $C^3$  256 vibrations per second,  $Sol^3$   $G^3$  384 vibrations per second may be sounded; for there being for every two waves of C three waves of G, there will be a coincidence for every second wave of C and every third wave of G. The next ratio being that of 3 to 4, or C and F,  $C^3$  and  $F^3$   $Fa^3$ , 341.3 vibrations per second, may be sounded together. Although we have already shown by the siren that the sounding of the notes C E G, together, give rise to the harmonious major chord, nevertheless, according to the law that the smaller the ratio of vibration between different sounds the more perfect the harmony, the combination of C with E—that is, in the ratio of 4 to 5, or, as in the above, of 256 to 320—is a less pleasing one than that of C to F, in which the ratio is 3 to 4. It is the want of harmony of F with G that excludes it from the cord C E G C; the cord C F A C is, however, a harmonious one. Continuing the next ratio, that of 6 to 5, or of C to E flat, a minor third, consistently with its ratio, being less simple than that obtaining in the major third, is a less harmonious one. Finally, as illustrating a step further the law just enumerated, it may be mentioned, though well known, that the interval corresponding to a tone in which the vibrations giving rise to the two notes  $C^3$   $D^3$ , for example, are in the ratio 8 to 9, 256 to 288 is a dissonant one, and that the interval of a semitone C to D flat, in which the ratio is 15 to 16, is a very sharp, grating, and dissonant one. About five hundred years before our era<sup>1</sup> it was shown by Pythagoras that if a stretched string was so divided into two parts that one was twice the length of the other, and the two parts of the string sounded simultaneously, that the note emitted by the short part was the octave emitted by the long one. Continuing to experiment, this celebrated philosopher next showed that if the string be divided in the ratio of 2 to 3 then the interval between the notes emitted would be that of a fifth; and further, that, according to the ratio in which the string was divided, the

<sup>1</sup> Montucla : Hist. des Mathematiques, Paris, An. vii. tome i. p. 114.

remaining more or less consonant intervals would be heard (Table LXXXII.), the harmony of the two sounds being proportional to the simplicity of the ratio of the two parts into which the string was divided.

TABLE LXXXII.

| Note . . . . .         | 1st. | 2d.           | 3d.           | 4th.          | 5th.          | 6th.          | 7th.           | 8th.          |
|------------------------|------|---------------|---------------|---------------|---------------|---------------|----------------|---------------|
|                        | C    | D             | E             | F             | G             | A             | B              | C             |
| Lengths of the string, | 1    | $\frac{8}{9}$ | $\frac{4}{5}$ | $\frac{3}{4}$ | $\frac{2}{3}$ | $\frac{3}{5}$ | $\frac{8}{15}$ | $\frac{1}{2}$ |
| Number of vibrations,  | 256  | 288           | 320           | 341           | 384           | 426           | 480            | 512           |

This important law, the first step made in the physical explanation of musical intervals, Pythagoras, however, did not account for, it remaining for later investigators to show that the vibrations of strings are inversely proportional to their lengths. It has just been mentioned that while the combination of a fundamental tone with its octave, for example, is a consonant, pleasing one, giving rise to no discord, that of the interval of a tone, or of a semitone, is a dissonant, disagreeable, discordant one. It remains for us now, therefore, to determine, if possible, the physical cause of discord. It will be remembered that in the double siren of Helmholtz there are two series of 12 orifices, each common to both sirens; such being the case, if both these series of orifices are opened and air forced through the instrument, the two sounds produced will be in unison, and will continue so, since the pitch of both will be the same however low or high the sound may be. In describing the double siren attention was also called to the fact that, by turning the handle of the upper siren the orifices of the wind chest will either meet or retreat from those of its retreating disk, the pitch of the upper siren rising or falling accordingly. But the relation of the rotation of the handle to that of the upper wind chest is such that if the handle be turned through 45 degrees the wind chest turns through 15 degrees, or through the  $\frac{1}{4}$ th of its circumference, which causes the orifices of the upper wind chest to be closed at exactly the same moment that the 12 orifices of the lower wind chest are opened, and *vice versâ*, the effect of which is that the intervals between the puffs of the lower siren—that is, the rarefactions of its sonorous waves—will be filled up by the puffs or condensations of the waves of the upper one. But if the condensation of the one set of sonorous waves coincides with the rarefactions of the other, set there will be neither condensation nor rarefaction, upon which all sound depends, the fundamental sounds of the siren will be extinguished through the interference of the two sounds, as it is called, and absolute silence would result were it not for the presence of the overtones of the siren. Rotating, however, the wind chest through 30 degrees, or the  $\frac{1}{2}$ th of its circumference, by turning the handle through 90 degrees, the puffs or condensations of the sonorous waves of the lower siren will coincide with those of the upper one, reinforcing the latter; and as this latter takes place once for each 90 degrees, there will be 4 of these reinforcements, or beats, as they are called, for every 360 degrees, or for one rotation of the handle.

The change in the pitch of the sound emitted by the upper siren induced by the rotating of the handle, the pitch of the sound emitted by the lower siren remaining the same, gives rise then to beats of



which there will be four for every one rotation of the handle. For a time, however, there may be heard twelve or eight beats; when such is the case, it is due to the strength of the second or first overtone being sufficient to overpower the fundamental, which vibrating three times and twice as rapidly as the fundamental, will, of course, give rise to three times, or twice as many beats. It is through the presence of these overtones that, though the tone of the fundamental may swell or sink as the handle is turned, sound is still heard, even though the handle reach the position at which the fundamental sound through interference is extinguished. Beats can be readily produced by tuning forks which are especially suited for this purpose, no overtones being generated if the forks be properly toned. Let us suppose, for example, that of two standard tuning forks  $Ut^3$ , each giving 256 vibrations per second, and whose sounds are therefore in unison, one of which be weighted just sufficiently to cause it to vibrate a little more slowly than the other, say 255 times. The two sounds then emitted will no longer flow on continuously in unison, there being now alternate diminutions and reinforcements of the sound or beats, and in this particular case one beat per second, which, it will be observed, is exactly the difference between the two rates of vibration of the two forks, 256 and 255. A moment's reflection will make it clear why the beats should occur, and at such a rate. Since the one fork vibrates 256 times in a second, and the other 255 times, it is evident that at the end of the second the wave of the latter fork will be one vibration behind that of the former, and at the end of the half second a half a wave behind, the one fork having made 128 vibrations, the other  $127\frac{1}{2}$ , but at that moment the condensation of the one wave coinciding with the rarefaction of the other, the sounds will be extinguished through their complete interference with each other. From the half of the second onward, however, until the end of the second, the condensations reinforce each other more and more, until at the end of the 256th vibration of the one fork, and the 255th of the other condensation coincides with condensation, and rarefaction with rarefaction, the full effect of both sounds being then experienced. Similarly, from the half second where the interference is complete backward to the beginning of the second, condensation coincides more and more with condensation, rarefaction with rarefaction, until at the beginning of the second, of course, as at the end, the coincidence is complete. Suppose, however, that the two forks vibrate 240 and 234 times a second, then at the end of the first  $\frac{1}{6}$ th of a second, one fork will have generated 40 sonorous waves, the other 39, the one wave being one vibration ahead of the other, and therefore, at the end of the  $\frac{1}{12}$ th of a second half, a vibration ahead. This instant being, however, that at which interference is complete, during which the sound is extinguished, the time elapsing on the one hand between it, or the  $\frac{1}{12}$ th of the second, and the beginning of the second, and on the other to the end of the  $\frac{1}{6}$ th of the second, will be characterized, as in the preceding case, by a gradual diminution, followed by a gradual augmentation of the sound or one beat; but as this is repeated in this case six times during the second, there will be six beats, which, it will be observed, is exactly the difference between

the two rates of the forks, 240 and 234. Experimenting this way with forks, pipes, etc., it can be proved that the number of beats per second is always equal to the difference between the rates of vibration of the two sounds to whose interference they are due. Now it has been shown by Helmholtz that if the beats per second succeed each other less rapidly than 33 per second, the sound is not disagreeable, but if at that rate, the dissonance becomes then absolutely intolerable. As the number of beats per second, however, increases, the dissonance diminishes, and when the beats have reached the rate of 132 a second, they disappear and discord vanishes. Beats are therefore the cause of dissonance or discord, and intervals free from them will be harmonious. Thus the fundamental, due, for example, to 256 vibrations per second, when continued with its octave due to 512 vibrations is a harmonious one, free from beats, since the difference in the rate of vibration, or 256, is too high to admit of them. The interval of the fifth C and G is still harmonious, the difference in the rate of vibration,  $384 - 256 = 128$ , being also too high. On the other hand, the interval of the fourth C and F due to 341 and 256 vibrations per second, respectively, is somewhat dissonant, the difference between the rates of vibration being 59, admitting, therefore, of that number of beats below the limits at which discord vanishes; and the interval of C and E more dissonant still, the difference in their rates of vibration being 64, the notes being due to 256 and 320 vibrations per second, respectively. It should be mentioned in this connection, in order to avoid any misconception, that the phenomenon of beats is of an entirely different nature from that of the resultant tones discovered by Sorge, Sartini, and Helmholtz. That resultant tones should ever have been considered as identical with beats, is not so strange, since the rate of vibration of the first difference tone, or the loudest resultant tones like that of beats, is equal to the difference in the rates of vibrations of the two primary sounds producing them, which led the celebrated Young to regard resultant tones as due to the linking together of rapidly recurring beats. Resultant tones are, however, produced in a totally different manner from beats, being due to the continuation of the secondary waves generated when the vibrations giving rise to the two sounds producing them are so intense as to exceed the ordinary law of the superposition of vibrations. That a resultant tone is not made up of beats, is shown by the fact that while a resultant tone due to thirty-three vibrations per second is smooth, consonant, musical beats succeeding each other at that rate, as already mentioned, are most dissonant.

In concluding this necessary digression upon the nature of musical intervals, discords, beats, resultant tones, etc., it must be observed that whether they are caused in the manner indicated, or however they may be accounted for physically, hereafter, in any case, no explanation whatever is offered why one rate of vibration should affect us agreeably, and another rate disagreeably—that is, if sounds are harmonious through the absence of discords, why should the presence of the latter give rise in us to a sense of discomfort, dissonance? Nor have we any reason to hope, judging from the past, that the study of mere acoustics will ever



throw any light upon our sensations of tone subjectively, or contribute to the progress of music objectively. Indeed, it appears to be generally forgotten by the cultivators of harmony, that the best music was composed when acoustics was in its infancy, to this day, the best illustration of theoretical harmony being taken from the works of Mozart, Handel, Haydn, and that according to one of the latest and highest authorities<sup>1</sup> the science of sound has "not added one cord or progression that was not known to Bach." Remarkable as are the properties of the tympanic membrane, and essential as it is undoubtedly in normal hearing, when it is remembered that it, together with the remaining part of the middle as well as the external ear, is only the intermediate means by which the terminal filaments of the auditory nerve are excited, it becomes intelligible why after the rupture or even absence of both membranes, hearing, though impaired, and appreciation of musical sounds are still possible. The innumerable and different kind of sonorous waves impinging upon the tympanic membrane and throwing it into vibration to be appreciated in consciousness as sounds, must be thence conducted to the vestibule of the internal ear. This is accomplished by the chain of ear bones stretching across the tympanum from the tympanic membrane to the foramen ovale of the vestibule. The ear bones, while three in number, in point of fact may be regarded physiologically as being equivalent to one long bone, vibrating to and fro with the tympanic membrane. That such is the case is not only shown by the manner in which the bones are articulated with each other, but from the fact that in the lower vertebrates the homologue of the stapes is a long rod-like bone, passing from the tympanic membrane to the vestibule, the homologue of the incus and malleus not being situated within the tympanum, but outside of it, entering into the formation of the lower jaw. That the stapes is pressed against the liquid of the vestibule by the movement of the tympanic membrane and ear bones can be shown experimentally, as by Helmholtz, by fitting a slender glass tube into the semicircular canal and filling the vestibule and part of the tube with water, when, through the forcing of the tympanic membrane inward, the water will be seen to rise nearly the  $\frac{1}{25}$ -th of an inch. On the other hand, the risk of tearing away the stapes from its attachment to the foramen ovale during the outward movement of the tympanic membrane is avoided through the cog-like joint between the malleus and the incus being loosened, no very great traction being then exerted upon the stapes. The movement upon the tympanic membrane and ear bones can be graphically studied, and recorded, as by Koenig,<sup>2</sup> by attaching a style to the incus or malleus, the tympanic membrane being thrown into vibration by two organ pipes, and the sound of the latter reinforced by a resonator.

#### STRUCTURE OF THE INTERNAL EAR.

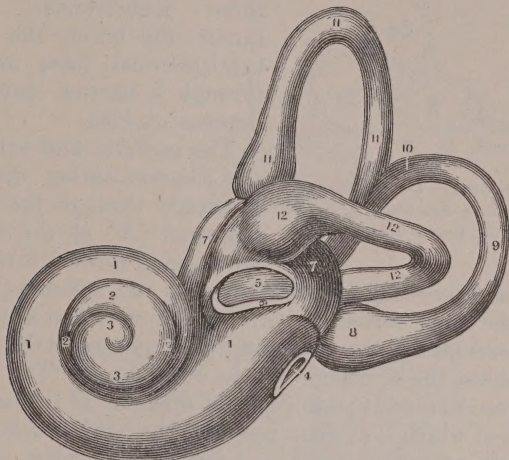
The internal ear includes the labyrinth and the auditory nerve. The labyrinth, so-called on account of its highly complex structure, consists of the vestibule, semicircular canals, and cochlea. Though these parts

<sup>1</sup> Hugh A. Clarke: *Harmony on the Induction Method*, Phil., 1880.

<sup>2</sup> Quelques: *Experiences d'Acoustique*, p. 29. Paris, 1882.

are imbedded in the petrous portion of the temporal bone, their osseous walls are independent of the bony structure of the latter. This is well seen at birth, when the whole labyrinth can be readily excavated from

FIG. 525.



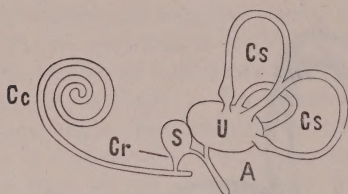
1, 2, 3. Turns of cochlea. 4. Fenestra rotunda. 5. Fenestra ovalis. 8, 9, 10. Posterior semicircular canal. 11. Superior semicircular canal. 12. External or horizontal semicircular canal.

the surrounding loose osseous substance. The vestibule, situated between the tympanum and the internal auditory meatus, is a somewhat oval-shaped cavity about the  $\frac{1}{5}$ th of an inch in diameter, passing postero-externally into the semicircular canals, and antero-internally into the cochlea, and communicating with the tympanum by the foramen ovale. The semicircular canals, so called on account of their form, are three in number and are named from their position superior, posterior, and inferior, or external, the two former being disposed vertically, the latter horizontally. Each semicircular canal expands at one extremity into a bottle-like dilatation, the ampulla, which communicates with the vestibule. Of the undilated extremities two unite, and then with the remaining one also open into the vestibule. The three semicircular canals thus communicate with the vestibule by five orifices. The vestibule, semicircular canals, and cochlea as well, are lined throughout with a thin periosteal membrane, which in passing over the foramen ovale and foramen rotundum thereby close these orifices. Within the cavity of this membrane is found a serous-like fluid, the liquor cœtemnii or perilymph of Breschet, an appropriate name on account of its surrounding the membranous labyrinth also containing a similar fluid, the endolymph of Breschet or liquor of Scarpa. The membranous labyrinth, so called on account of its membranous structure, and receiving the terminal filaments of the internal auditory nerve, floats in the perilymph within the bony labyrinth, with the walls of which it is more or less connected by delicate fibrous bands. The membranous labyrinth, like the osseous, consists of three parts, vestibule, semicircular canals,



and cochlea. The membranous vestibule (Fig. 526), however, is composed of two distinct sacs or pouches, the utriculus (U) and sacculus

FIG. 526.



Membranous labyrinth. Cs. Semicircular canals. U. Utriculus. S. Sacculus. A. Aqueduct of vestibule. Cr. Ductus reuniens. Co. Cochlea.

(S), the former of which, the larger, occupies the hemi-elliptical fossa of the bony vestibule, and gives off three membranous semicircular canals, the latter, the smaller, the hemispherical fossa and gives off through a narrow duct the membranous cochlea.

The sacculus and utriculus, while not communicating directly, do so indirectly through the membranous aqueduct (A) of the vestibule, the latter being formed through union of

the small ducts proceeding from the sacculus and utriculus, respectively. Adhering to the inner surface of both the utriculus and sacculus, may be seen white, discoidal masses, consisting of minute crystalline particles of calcium carbonate, the so-called otoliths or otocoma. The membranous, semicircular canals, about one-third of the diameter of the osseous ones, in the perilymph of which they float, resemble the latter in form and general disposition, being three in number, disposed superiorly, vertically, and horizontally, expanding into ampullæ, and communicating with the membranous vestibule by five orifices. The membranous vestibule and semicircular canals, consisting of three layers, an outer fibrous, an inner epithelial, and an intermediate membrana propria, receive, as already mentioned, the terminal filaments of the vestibular branch of the internal auditory nerve. The latter divides at the bottom of the internal auditory meatus into three branches, the first of which, passing through the pyramidal eminence of the bony vestibule at the superior cribriform spot, is distributed to the utriculus and ampullæ of the superior and inferior or horizontal semicircular canals; the second passing through the hemispherical fossa at the middle cribriform spot, is distributed to the sacculus; and the third through the ampulla of the bony posterior semicircular canal at the inferior cribriform spot, to the ampulla of the membranous posterior semicircular canal. Just in those situations where the nerve fibres penetrate the membranous vestibule (macula acustica) and the membranous semicircular canals (crista acustica), their outer or fibrous layer is intimately associated through connective tissue with the bony wall of the vestibule and canals, the perilymph being here absent. The ultimate nerve fibres having passed through the membranous vestibule and canals, finally terminate in what may be called the auditory epithelium, which appears to consist essentially of columnar cells intermixed with spindle-shaped ones supporting long, firm bristles, the auditory hairs (Fig. 527), which penetrate into the soft otolith mass supporting the otoliths and the endolymph. Up to the present moment, in order to prevent confusion, we have purposely avoided mentioning, except incidentally, the bony or membranous cochlea, and yet it will be found that the cochlea, though, at first sight, resembling but little a semicircular canal, consists, like the latter, of a bony tube enclosing and attached to a membranous one, the latter floating in perilymph and con-

taining endolymph. For simplicity sake, let us, in considering the structure of the cochlea, begin by disabusing our minds of it being a coiled tube, and regard it as a straight one, as it is throughout its whole

FIG. 527.

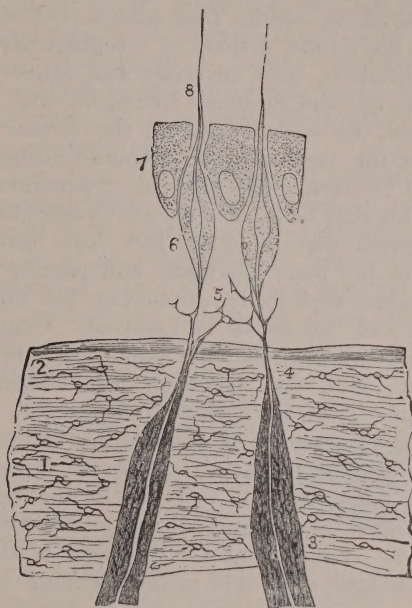
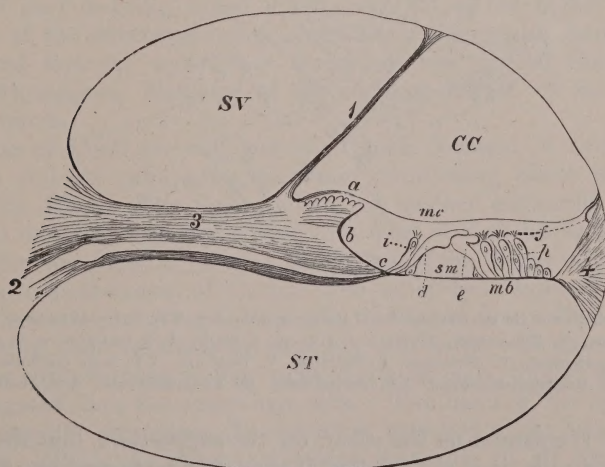


Diagram of the auditory epithelium, and the mode of termination of the nerves of the ampullæ. 6. Spindle-shaped cells, each supporting an auditory hair (8). 7. Basal supporting cells. 3, 4. Nerve fibre passing through the tunica propria to join the plexus in the epithelium. (M. SCHULTZE.)

FIG. 528.

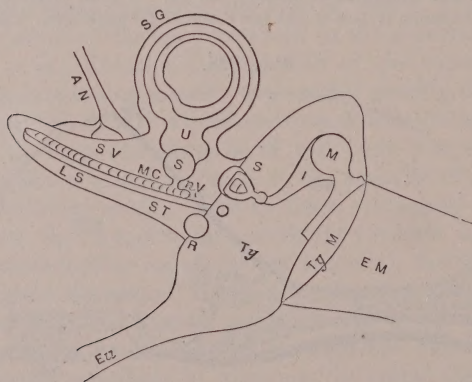


Section through one of the coils of the cochlea, diagrammatic. Mag. 30. ST. Scala tympani. SV. Scala vestibuli. CC. Canalis cochleæ. 1. Membrane of Reissner forming its vestibular wall. a. Limbus laminæ spiralis. b. Sulcus spiralis. 3. Cochlear nerve. mc. Membrana tectoria. mb. Membrana basilaris. d e. Rods of Corti. 4. Ligamentum spirale.



length in birds, and at its commencement in man ; and further, let us begin our description of its structure by supposing that we are viewing the cochlea at its commencement in transverse section, as obtained by dividing the vestibule along the line passing over 9 (Fig. 525), and looking at the cochlear portion of the section endwise, as represented in Fig. 528. Looking at the cochlea from such a point of view, it will be seen to consist of a bony tube, divided by a septum partly bony (lamina ossea), partly membranous, into an outer and inner space, the latter communicating through the foramen rotundum with the tympanum, and called, therefore, the scala tympani ; the former continuous with the bony cavity of the vestibule, and communicating, therefore, indirectly through the foramen ovale with the tympanum, and called the scala vestibuli. This may be at once shown by readjusting the cochlear portion of the section that we have just been considering to the remaining portion of the bony labyrinth, and passing bristles through the foramen rotundum and ovale, supposing the membrane passing across this opening and the stapes be removed. Conceiving, however, that the cochlea be a straight tube, and supposing it to be divided longitudinally, it will be found that the bony, membranous partition (Fig. 529) is absent at the end of the cochlea (helicotrema), the end opposite to the vestibule, the consequence of which is that the bristles just passed through the foramen ovale from the tympanum, if continued onward, after traversing the scala vestibuli, will pass at the end of the cochlea into the scala tympani, and thence, through the foramen rotundum, reach the tympanum. Such being the relations of the scala vestibuli and scala tympani to each other and to the vestibule on the one hand,

FIG. 529.



Diagrammatic view of the relative position of the parts of the ear. EM. External meatus, Ty M. Tympanic membrane, Ty. Tympanum, M. Malleus, I. Incus, S. Stapes, R. Round window, O. Oval window, SG. Semicircular canal, U. Utriculus, S. Sacculus, V. Vestibule, SV. Scala vestibuli, ST. Scala tympani, MC. Membranous cochlea, LS. Lamina ossea, Eu. Eustachian tube, AN. Auditory nerve.

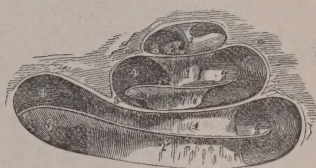
and to the tympanum on the other, on the supposition that the cochlea is a straight tube, it is obvious that if the latter be turned two and a half times upon itself around an axis or modiolus from right to left in the right ear, and the reverse in the left, the apex being situated downward,

forward, and outward, that the above relations will not in any way be essentially changed. From an inspection of Fig. 528, representing the cochlea in transverse section, it will be observed, however, that the membranous portion of the septum dividing the interior of the cochlea into the scala vestibuli and scala tympani, and attached to the osseous wall by the ligamentum spirali, consists of two layers, a basilar membrane, and a tectonal membrane, a space intervening between the two, and that just at the point where the tectonal membrane is attached to the osseous lamina, which in the coiled tube is, of course, spirally disposed, a third membrane, the membrane of Reissner, passes obliquely across to the outer osseous wall.

As a matter of fact, however, in nature, at both ends of the cochlea, through the space intervening between the basilar and Reissner membranes, being covered in by membrane, the vestibular scala is separated from the tympanic scala by a membranous tube which is given off by the membranous sacculus (Fig. 529) through the ductus reuniens *n*, just as the membranous semicircular canals are given off by the utriculus, the other end of the membranous cochlear tube being attached by its pointed blind extremity to the wall of the cupola, the latter partly bounding the helicotrema. And just as the membranous semicircular canal, filled with endolymph and floating in perilymph, is attached to the wall of the bony semicircular canal, so is the membranous cochlea, filled with endolymph and floating in perilymph, attached to the wall of the bony cochlea, the membranous cochlea, however, being spirally disposed like the bony cochlea enclosing it (Fig. 530). The membranous cochlea differs, however, from the membranous semicircular canal, not only in being coiled upon itself, but in the highly complex character of the structures lying in the space intervening between the basilar and tectonal membranes, known as the rods of Corti, which receive the terminal filaments of the cochlear branch of the internal auditory nerve.

The rods of Corti are stiff, rod-like bodies, disposed in two sets, an inner set and an outer set; the inner numbering about 6000, the outer about 4500. The inner rods being inclined outwardly, and the outer rods inwardly, the two sets of rods meet at their heads, the space between the rods—that is, between the latter and the basilar membrane—being known as the canal of Corti. The inner rods support on their inner surface one row of epithelial cells, the inner hair cells, so called, on account of their terminating in short, stiff hairs; the outer rods on their outer surface three or four rows of similar cells, though somewhat more elongated than the outer hair cells. The hairs of the latter pass through ring-like structures, the reticulum, attached to the heads of the outer rods. Both the outer and outer hair cells, in all probability, receive, directly or indirectly, the terminal filaments of the cochlear nerve (Fig. 531). The latter, after passing through the foramina of the spiral tract at the bottom of the internal auditory meatus, ascend through

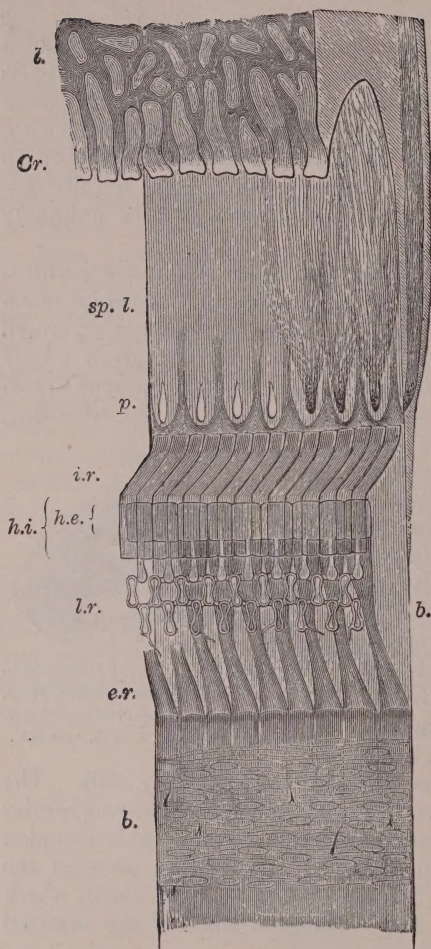
FIG. 530.



Diagrammatic view of the osseous cochlea laid open. 1. Modiolus or central pillar. 2. Placed on three turns of the lamina spiralis. 3. Scala tympani. 4. Scala vestibuli.



FIG. 531.



Semi-diagrammatic view of part of the basilar membrane and tunnel of Corti of the rabbit, from above and the side. Much magnified. *l.* Limbus. *Cr.* Extremity or crest of limbus with teeth-like projections. *b, b.* Basilar membrane. *p.* Perforations for transmission of nerve fibres *N*, which are represented at the lower part of the figure, but omitted for the sake of clearness in the upper. *i, r.* Fifteen of the inner rods of Corti. *h, i.* Their flattened heads seen from above. *e, r.* Nine outer rods of Corti. *h, c.* Their heads, with the phalangeal processes extending outward from them and forming with the two rows of phalanges, the lamina reticularis. *t, r.* The fibres of the outer rods are seen to be continued into the striation of the basilar membrane, through which the connective tissue fibres and nuclei of the undermost layer are seen. Portions of a few of the basilar processes of the outer hair-cells remain attached to the membrane. (QUAIN and SHARPEY.)

the axis of the cochlea, and thence traversing the lamina ossea spiralis perforate the basilar membrane, and so reach, by intermediate filaments, the hair cells, bearing in mind that the base of the stapes is adherent to the periosteum lining the vestibule and covering the foramen ovale; it is evident that the vibrations of the tympanic membrane, in being transmitted through the ear bones to the perilymph filling the bony labyrinth, will throw into vibration the endolymph filling the membranous labyrinth and the hairs projecting into it, and consequently the auditory nerve, regarding, as we do, the hairs as the terminal filaments of the vestibular and cochlear nerves, into which the auditory nerve divides in the meatus, whence the vibrations, in being further transmitted to the temporo-sphenoidal convolutions of the cerebrum, give rise to the sensation and perception of the sound. With reference to the function of the membrane covering the foramen rotundum, the membrana secundaria, which consists on the tympanic side of the mucous membrane, and on the cochlear of the periosteal layer lining the scala tympani of the cochlea; while nothing is positively known, in all probability it is pushed outward, as the stapes is pushed inward, which would obviously be of advantage in absorbing some, at least, of the superfluous sonorous wave motion. Such being, in general, the disposition and relation of the parts of which the internal ear is composed, and the manner in which the auditory nerve is distributed to it, is thrown

into vibration, it is to be expected that such a complexity of structure is correlated with a corresponding differentiation in function. As a matter of fact, however, nothing has been definitely established as regards the specific functions of the vestibule, semicircular canals, and cochlea, which is due, no doubt, to any experimental investigation being so difficult on account of the nature of the case, and from the pathological and clinical data on the subject being so meagre and unreliable in character. In the absence of such evidence the facts of comparative anatomy alone remain as a means of elucidating the functions of the internal ear. It is well known to anatomists that the organ of hearing exists in the lower animals in a very rudimentary condition; thus, in certain of the crustacea, for example, the ear consists of an invagination of the skin, a cutaneous pit lined with hairs, situated in the basal joint of the internal antennæ, which may remain open, and contain particles of sand, or may be closed and enclose calcareous otoliths. A similar vesicle, lined with ciliated epithelium, and containing otoliths, is also found in the mollusca situated upon the infra-oesophageal portion of the nervous collar surrounding the alimentary canal. On the supposition that the vesicle just described as occurring in the crustacea and mollusca, and even in lower forms of life, as in the annelida, hydrozoa, etc., is a rudimentary organ of hearing, its functions must be limited almost entirely to the appreciation of the intensity or loudness of sounds—at least it is difficult to conceive of animals relatively so lowly organized being affected to any very great extent by difference in pitch and quality. If such is the case, and it be admitted that this vesicle, or otocyst of the lower animals, is the homologue of the vestibule of the higher, which the study of the development leads us to suppose, then it follows that the function of the vestibule in man is the appreciation of the intensity of sound. In passing from the invertebrata to the vertebrata, and more particularly to the fishes, we find, with the exception of the amphioxus, in which the ear is absent altogether, that the organ of hearing becomes more complex as we ascend through the successive forms of piscine life. Thus, in the myxine, the ear consists of a vestibule with one semicircular canal; in the lamprey of a vestibule with two semicircular canals; and in the teliosts of three with a rudimentary cochlea as well. Now, while it is evident that it would be of advantage to fishes to be able, not only to distinguish loud from low sounds, but also the direction from which the sounds proceed, the appreciation of melodious and harmonious ones would be of no use, and since the homology of the semicircular canals of the lower vertebrates with those of the higher ones is undoubted, in all probability our appreciation of the direction and distance of sounds, which is very much a matter of education, is connected in some way with these structures, experiments, and pathological facts, already referred, to prove conclusively that injury of the semicircular canals involves disorders of equilibrium. To what extent the latter are due to the hearing being impaired, and how much to the transmission of the afferent impressions to the cerebellum being interfered with, upon which the maintenance of equilibrium partly depends, is difficult, if not impossible, to determine exactly. By a method of exclusion, then, the inference is rather forced upon us, that



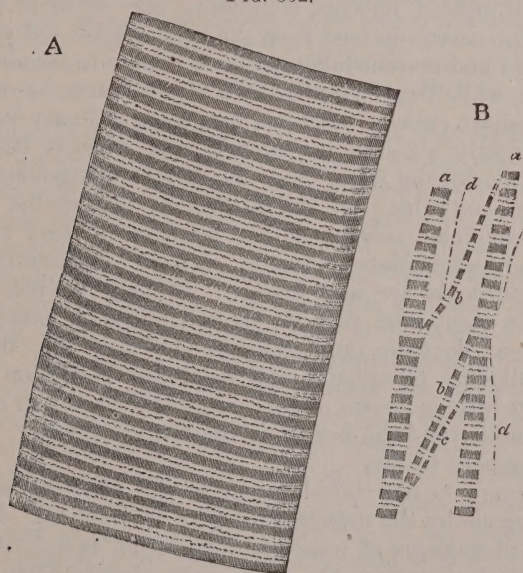
our sensation of tone depends, in some way, upon the cochlea, the structure of which undoubtedly suggests that its function is rather concerned with the appreciation of the quality of sound, a sort of universal resonator, than with that of pitch or intensity. Regarding the rods of Corti, and the hair cells lying upon them, as so many piano keys and strings appropriately tuned, it is obvious that it would analyze sounds, like our series of resonators. The objection to the above ingenious view of Helmholtz, that the cochlea in birds is very rudimentary, is not a necessarily fatal one, since, though many birds can sing, it does not follow that their sensations and ideas of melody and harmony should be as developed as that of man; on the contrary, in the absence of a complex brain it is difficult to comprehend how they should have any considerable appreciation of musical sound. In conclusion, it must not be forgotten that whatever function, if any, be assigned to the different parts of the internal ear, that the cause of the sensation of sound, like that of color, lies in the brain, and in its subjective aspect is as little understood in the one case as the other.

## CHAPTER LIV.

### MUSCULAR CONTRACTILITY.

IN considering the subject of nervous irritability, it will be remembered that the contraction of a muscle following stimulation of the nerve supplying it, was taken as an indication and measure of the changes occurring in the latter. The changes undergone by the muscle itself, however, during its contraction remain still to be described. Muscles are of two kinds, striped and unstriped, of which the former will be first studied. Striped muscles, such as the skeletal muscles, heart, diaphragm, etc., consist of fasciculi or bundles of fibres separated by connective tissue, the latter being prolonged from the outer envelope or perimysium covering the muscle. Each muscular fibre is a more or less cylindrical tube from 3 to 4 cm. ( $1.2$  to  $1.6$  of an inch) in length, and between  $\frac{1}{4}$ th and  $\frac{1}{24}$ th of a mm. ( $\frac{1}{100}$ th and  $\frac{1}{600}$ th of an inch) in

FIG. 532.



A. Portion of a medium-sized human muscular fibre (magnified nearly 800 diameters). B, separated bundles of fibrils, equally magnified; *a*, *a*, larger, and *b*, *b*, smaller collections; *c*, still smaller; *d*, *d*, the smallest which could be detached. (KIRKES.)

diameter, and consists of three parts, the sarcolemma or sheath, the sarcous substance, and the nuclei or muscle corpuscles. The sarcolemma is the elastic, transparent, structureless, and colorless sheath enclosing the sarcous substance. The latter being marked transversely by

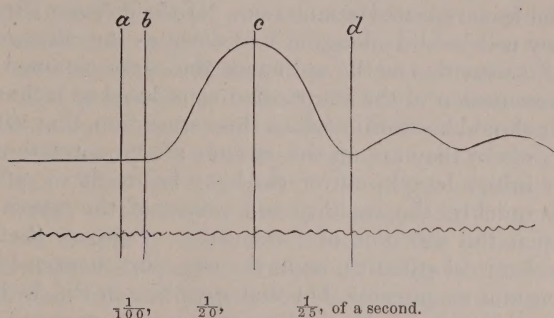


alternating light and dark bands, is said to be transversely striate. If fresh muscular fibre be examined in its own juice, not only the light and dark bands just referred to will be seen, but it will be observed (Fig. 532) that the light band is divided into two by what looks like a line, but which seems to be in reality the edge of the membrane, running transversely across the fibre and attached all around to the sarcolemma, through which each fibre is divided into a series of compartments placed end to end. It is within these compartments that the sarcous substance is situated. The latter consists of a broad, dim, doubly refracting (anisotropic) contractile disk, both ends of which are capped by a layer of clear, homogeneous, refracting (isotropic) soft or fluid substance. The nuclei or muscle corpuscles lie immediately under the sarcolemma, their long axis being in the long axis of the fibre, and in all probability generate the sarcous substance. As already mentioned, muscles being active organs are well supplied with blood, and with sensory as well as motor nerves; the sensibility of muscles is relatively, however, but slight. The second variety of muscle, the non-striated or smooth, occurring among other situations in the alimentary canal, arteries, ureter, etc., consists of fusiform or spindle-shaped cells with tapering ends, varying in length from 45 to 230 mic. mm. ( $\frac{1}{600}$ th to  $\frac{1}{120}$ th inch) in breadth, from 4 to 10 mic. mm. ( $\frac{1}{6000}$ th to  $\frac{1}{2500}$ th inch). Within each cell may be seen after the addition of acetic acid, a solid, oval, elongated nucleus, containing one or more nucleoli, in which the motor nerves derived from the sympathetic and consisting of both medullated and non-medullated fibres, appear to terminate. Non-striated muscle, while freely supplied with blood, is not, however, so vascular as the striated variety. Striated muscle or ordinary flesh is either neutral or slightly alkaline in reaction, and consists chemically by weight, of three-fourths water and one-fourth nitrogenous, non-nitrogenous matters, and salts. Of the nitrogenous matters the most important is the coagulable substance that becomes in dead rigid muscle myosin, though albuminates, creatin, xanthin, hypoxanthin, taurin, inosic and uric acids are also present. Among the non-nitrogenous matters may be mentioned para or sarco, lactic acid, mosete or muscle sugar, glycogen, dextrine, and glucose. Of the salts, the principal ones are the alkaline phosphates and sulphates, potassium and sodium chloride. But little is known of the chemical composition of unstriated muscular tissue, beyond the fact of it consisting of water, nitrogenous and non-nitrogenous bodies.

Let us turn now to the consideration of the physical and chemical changes undergone by the muscle during its contraction. Many of the most striking phenomena of muscular contraction as well as the method of observing and recording the same, have already been incidentally demonstrated in considering nervous irritability. It will be remembered, that by attaching a lever to a muscle and connecting the pen of the same with the recording cylinder or the plate of the pendulum myograph, that we obtained a trace (Fig. 533), that of the muscle curve, and that by means of suitable chronographic apparatus we determine the latent period, the time intervening between the beginning, the maximum, and the end of the contraction, the curve of tetanus, etc.

Further, by means of the galvanometer and differential rheotome, it was shown that during a period of rest, the nerve exhibited an electrical current, but that during its excitement the electrical current disappeared, and the nerve current appeared, the rate of disappearance of the one being the same as that of the appearance of the other. It will only be necessary, therefore, in this connection, after

FIG. 533.



A muscle-curve obtained by means of the pendulum myograph. To be read from left to right. *a* indicates the moment at which the induction-shock is sent into the nerve, *b* the commencement, *c* the maximum, and *d* the close of the contraction. The two smaller curves succeeding the larger one are due to oscillations of the lever. Below the muscle-curve is the curve drawn by a tuning-fork making 180 double vibrations a second, each complete curve representing therefore  $\frac{1}{180}$ th of a second. It will be observed that the plate of the myograph was travelling more rapidly toward the close than at the beginning of the contraction, as shown by the greater length of the vibration-curves. (FOSTER.)

recalling what has already been said, to repeat that there is a negative variation of the electrical current of muscle during the activity of the latter, and to add that this negativity, as shown by Bernstein,<sup>1</sup> travelling at the rate of 3 metres (9.8 feet) a second, with an average length of 10 millimetres, is immediately followed by or transmitted into a visible contraction wave, the muscle impulse travelling at its heels at about the same rate, but with a wave length of from 200 to 400 millimetres, which causes the muscular fibre as it passes over it to swell and shorten. If a portion of living irritable muscle of an insect, that of *Telephorus*, for example, be viewed under the microscope, the contraction waves observed passing along the fibres may be fixed by appropriate treatment with osmic acid, and so compared with the remaining portion of the fibre at rest. By such method of investigation, it has been shown, that while the dark and light bands so characteristic of striated muscle at rest are still observable in the muscle when contracted, the relation of the two is reversed, that is to say, the dark band in the contracted muscle corresponds to the light band in the quiet one, and vice versa, the distinction between light and dark bands not being observable, however, during the intermediate stage between rest and contraction. While there is still some difference of opinion as to the interpretation of all of the appearances of such a preparation, the same

<sup>1</sup> Untersuchungen, S. 58. Heidelberg, 1871.



makes very evident the swelling and shortening of the fibres, which is brought out even better if the object be viewed by polarized light.

In describing the induction apparatus of Du Bois-Reymond, it will be remembered that the secondary coil can be removed as desired from the primary and the strength of the stimulus thrown into the nerve or muscle in this way varied. Beginning with a very weak stimulus and gradually increasing the same, the corresponding contraction will be found to increase, at first rapidly then more slowly until a maximum is reached, then to diminish until contraction finally ceases through the muscle being fatigued from repeated stimulation. If the distance through which the secondary coil be slid along be laid down as the abscissa line and the extent of contraction as the ordinates, the curve obtained will be the graphic representation of the contraction considered as a function of the stimulus. It should be mentioned, in this connection, that while muscles in the body, where they are on the stretch after contraction, return at once to their initial length, out of the body fail to do so either as completely or as quickly, the rapidity and extent of the return appearing to depend upon the nutrition of the muscle. Suppose that instead of varying the electrical stimulus, as in the case just mentioned, we maintain it as constant as possible, but that we place in the little scale pan suspended from the lever attached to the muscle successively 10, 20, 30, 40, and 50 grammes—that is, we gradually increase the weight the muscle has to lift to increase the resistance that it has to overcome. Contrary to what might naturally be expected, the resistance offered to the contraction, for a time at least, increases the contraction, then with a continued increase of weight, the contraction having reached a maximum, gradually diminishes until finally it ceases altogether. If the weights be regarded as the abscissas and the extent of contraction as the ordinates, then the curve obtained will represent the contraction regarded as a function of the resistance. It will be observed, in experimenting with weights, that a stretched muscle reaches quickly its initial length after the extending cause has been removed, the elasticity not being very great but perfect. Contrary, however, to what might have been expected, the extensibility is not diminished during contraction but increased, so that the muscle has to overcome the resistance due to its extensibility before it can raise any weight. Thus, suppose that a muscle be extended a given extent by a weight of say 40 grammes during rest, and then that it be unloaded and thrown into a state of tetanus and then again loaded with the same weight, the extension in the latter case will be greater than in the former. It will also be learned, by experimenting with gradually increasing weights, that finally the elongation of the muscle due to its elasticity is exactly compensated by the shortening due to its contraction, such a contraction of static equilibrium being reached in the case of the frog, the transverse section being one square centimetre and the weight 692 grammes, and in man, the muscles being those of the calf of the leg, and the weight 8 kilogrammes (17.6 lbs.).

The work done by a muscle, like all work, is estimated by the height through which a weight is raised. Thus, if 5 grammes (77.1 grains) are raised 27 millimetres (1.08 inch) by the muscle of a frog, then  $27 \times 5$ ,

135 grammes millimetres (83 grain inch) work is done by such a muscle. By gradually increasing the weights and noting the heights through which they are raised, it will be found that the work done gradually increases as the weight increases until a maximum is reached, after which there is a gradual diminution until the muscle, as in the former instances, ceases to contract. The fatigue experienced by muscle during prolonged contraction, which sooner or later brings the latter to an end, appears to be due to the accumulation of the waste effete products incidental to its activity. Within certain limits such matters are eliminated as rapidly as formed and new materials for the repair of the muscle are at the same time supplied. If, however, the contractions follow each other very rapidly, sufficient time is not allowed for the accomplishing of these processes, and the equilibrium between disassimilation and assimilation is no longer maintained. While the cohesion and irritability of muscle are diminished by fatigue, the elasticity is but little, if at all, affected. The latent period is, however, lengthened. During fatigue the extent of contraction is smaller and the latter lasts longer than when the muscle is fresh, the return to the initial length is also slower. As might be expected, a muscle is fatigued much sooner when it does work than when it simply contracts without doing work. If a stethoscope or myophone be applied over a powerfully contracting muscle, the biceps, for example, a deep, low tone will be heard, the pitch of which is about 40 vibrations a second, and which is, without doubt, due to the successive shortenings which make up a muscular contraction, the latter caused, in all probability, by 40 nervous impulses being transmitted to the nerve centres along the motor nerves to the muscle. We say that the pitch of this muscular sound or tone is 40 vibrations per second and caused by 40 nervous impulses, because that is the note actually heard, and because we can produce such a note experimentally out of the body by stimulating the nerve that number of times, or a note due to 80 vibrations per second by stimulating the nerve that number of times.

It should be mentioned, however, that according to most physiologists, the muscular sound heard when the biceps contracts, while due to 40 vibrations per second, is really the first overtone or first octave above the fundamental, the latter being due to 20 vibrations per second. If such be the case, then the muscle contracts only 20 times a second, the pitch of the muscular sound produced is 20 vibrations a second, and the nerve is stimulated 20 times a second. Whether the muscular sound heard be the fundamental note or the octave above, in either case, however, the mechanism of its production is the same—that is, due to muscular vibration. It will be remembered that in accounting for the first sound of the heart, muscular contraction was assigned as one of the causes, and while there is no doubt that it is an element in the production of the first sound, it must be admitted that it is difficult to understand how the contraction of the heart, if a simple one, can give rise to a muscular sound, which we have just seen is produced by numerous contractions. Facts of this kind, as well as peculiarities in the muscular structure of the heart itself, lead one to suppose that possibly the contraction of the heart during its ventricular systole



is rather of a tetanic than simple character, as is usually supposed. The muscle sound or muscle tone due to successive muscular contractions must not be confounded with what is unfortunately called muscular tonus or muscular tonicity, by which is meant the state of tension due to the muscles in the living body being more or less stretched between their attachments. Such being the case, when a muscle is divided transversely it contracts, the two parts receding from each other. The sphincter muscles, however, do not appear to be stretched during repose, but only when they are dilated. On the other hand, by the term muscular tone, as understood more especially by neurologists, is meant the firmness or tone of muscle due to continued nervous excitement emanating from the spinal cord. By some physiologists, however, it is denied that the spinal cord exerts any such tonic influence upon the muscles, and yet it is well known that a decapitated frog will remain in a sitting posture as long as the spinal cord is intact, but that with its removal the limbs fall apart. Further, the limbs of a decapitated turtle, and, to a certain extent, those of a decapitated rabbit, also retain their firmness, tone, but with the removal of the spinal cord become lax, flaccid. Such facts are incomprehensible, unless it be supposed that the muscles are maintained firm, elastic, resilient, through the influence of the spinal cord. As the influence exerted by heat, blood supply, etc., upon the activity of the muscle is essentially the same in the case of muscle as in that of nerve, it will not be necessary to dwell further upon the same in this connection. If living contractile frog's muscle, freed as much as possible from blood, be frozen and then minced and rubbed up in a mortar with four times its weight of snow containing 1 per cent. of sodium chloride, a mixture will be obtained, which at about 0° Cent., can be filtered. The filtrate so obtained, or muscle plasma, at first fluid becomes at ordinary temperature, jelly-like, and then separates into a clot and serum, the action which before coagulation was neutral, or slightly alkaline, now being distinctly acid. The serum contains albumen and extractives; the clot consists of myosin, a substance intermediate in character between fibrin and globulin. It will be observed, as in the case of the fibrin of the blood, that myosin does not exist as such in living contractile muscle, but that it is developed during the coagulation of the same out of some preëxisting albuminous element or elements. The myosin so developed from living muscle does not differ at all from the myosin obtained by appropriate chemical manipulation from dead muscle. Indeed, the passage of a muscle into the condition of rigor mortis, characterized by loss of its irritability, softness, translucency, extensibility, and elasticity may be regarded as being essentially due to the coagulation of its muscle plasma, to the development of myosin out of its preëxisting albuminous elements. Since living muscle during its contraction becomes distinctly acid from having been previously faintly alkaline or neutral from a considerable amount of carbonic and lactic, or sarcolactic acid being set free, as in the condition of rigor mortis, from the fact of the muscle, as in the latter distinction, becoming rigid, it might, at first thought, be supposed that the changes occurring during the contraction of the living muscle are

essentially the same as those occurring in rigor mortis, due to the oxidation of some complex albuminous material elaborated and stored up in the muscle during its periods of repose. That the phenomenon of muscular contraction is not, however, identical with that of rigor mortis, is shown by the important fact that during muscular contraction no myosin is developed, upon the formation of which the phenomenon of rigor mortis depends, and that during contraction the extensibility of the muscle is increased, instead of being diminished, and that it does not lose its translucency.

But little is positively known as to the physical and chemical changes undergone by unstriated muscular fibre during death or contraction; from what has been established, however, we are led to believe that the processes going on in unstriated muscle fibre differ in degree rather than in kind from those just described as occurring in striated muscle. While the limits of this work do not permit of any discussion of general muscular movements which would involve a detailed description of the muscles and joints and the consideration of animal mechanics, a brief account of how ordinary movements are performed does not appear inappropriate in concluding this chapter. The greater part of the skeletal muscles may be regarded as so many sources of power for moving the bones viewed as levers. The levers are of three kinds or orders according to the relative position of the power, the weight to be moved, and the axis of motion or fulcrum. In a lever of the first kind, as in Fig. 534, A, the

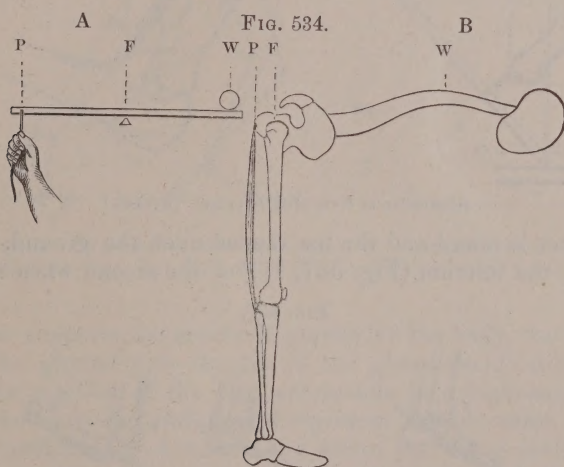


Illustration of lever of first order. (KIRKES.)

power (P) is at one end, the weight (W) at the other, and the fulcrum (F) in the middle. As a familiar example of the first kind of lever, occurring in the human body, may be mentioned the raising of the body from the stooping posture by the action of the hamstring muscles attached to the tuberosity of the ischium (Fig. 534, B). In a lever of the second kind (Fig. 535, A), the power is at one end, the fulcrum at the other, and the weight in the middle. The depression of the lower jaw in the opening of the mouth is an illustration of a lever of the second kind (Fig. 535, B),



in which the tension of the muscles elevating the jaw represents the weight. In a lever of the third kind (Fig. 536, A), while the fulcrum and weight are at either end, the power is in the middle. The flexing of the forearm by the action of the biceps muscle (Fig. 536, B) is an

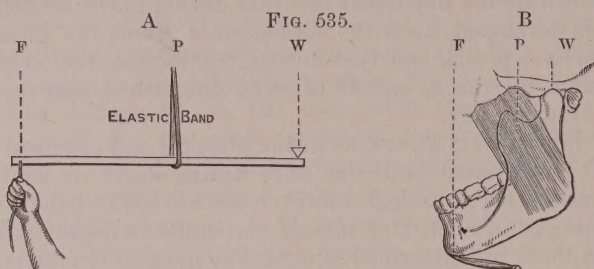


Illustration of lever of second order. (KIRKES.)

instance of this form of lever in the body. The different movements of the foot offer an illustration of all three kinds of levers: of the first kind

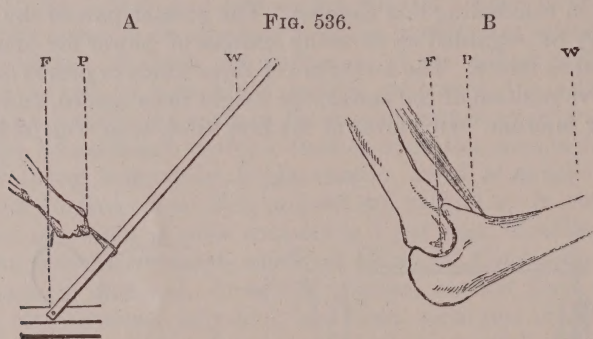


Illustration of lever of third order. (KIRKES.)

when the foot is raised and the toe tapped upon the ground, the ankle-joint being the fulcrum (Fig. 537, I); of the second when the body is

FIG. 537.

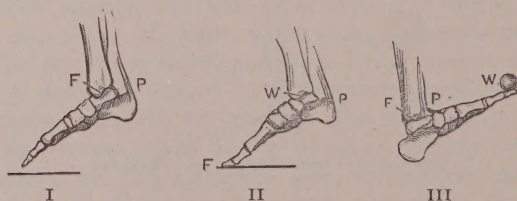


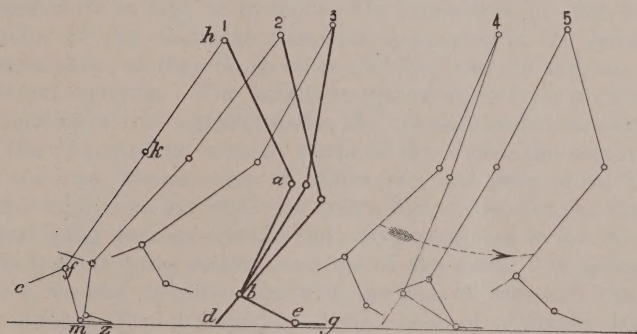
Illustration of levers of all three orders.

W. Weight of resistance. F. Fulcrum. P. Power. (HUXLEY.)

raised upon the toes, the ground being the fulcrum (Fig. 537, II); of the third kind, when one dances a weight up and down by moving only the foot, the fulcrum being the ankle-joint (Fig. 537, III). As a general rule, in the human body, the power is so disposed with reference to the fulcrum, that while a greater range of motion is acquired the power is diminished. Thus, in the case of the action of the biceps, it is evident

that a great amount of force must be put forth to move the forearm, but that a considerable range of movement is obtained through a relatively slight shortening of the muscular fibres. In the act of standing, as accomplished by muscular action, the body is in a vertical position of equilibrium, a line drawn from the centre of gravity of the body falling within the feet placed upon the ground. The head being firmly fixed upon the vertebral column by the cervical muscles pulling from the latter upon the occiput, and the vertebral column itself being fixed by the longissimus dorsi and quadratus lumborum muscles. In the sitting position, the head and trunk together constituting an immovable column, are supported upon the tubera ischii. In the forward posture the line of gravity passes in front, in the backward posture behind, and during the erect posture between the tubera ischii. In walking, the two legs act alternately, the one leg, the active or supporting leg, carrying the trunk, the other leg being inactive or passive. The act of walking, for convenience of description, may be considered as made up of two acts. Act 1st (Fig. 538): the active leg being vertical and slightly flexed at the

FIG. 538.



Phases of walking. The thick lines represent the active, the thin the passive leg. *h*. The hip-joint. *k*, *a*. Knee. *f*, *b*. Ankle. *c*, *d*. Heel. *m*, *e*. Ball of the tarso-metatarsal joints. *z*, *g*. Point of great toe. (LANDOIS.)

knee, alone supports the centre of gravity of the body, the passive leg touching the ground with the tip of the great toe (2) only. At this moment the position of the leg corresponds to a right-angle triangle in which the active leg and ground represent the two sides, the passive leg the hypotenuse. Act 2d: the active leg being inclined, moves forward to an oblique position, the trunk moves forward, the active leg being at the same time lengthened that the trunk may remain at the same height. The latter is accomplished by extension of the knee (3, 4, 5), and the lifting of the heel from the ground (4, 5), until the foot finally rests upon the ground by the point of the great toe. As the active leg is extended and moves forward the tips of the toes of the passive leg leave the ground (3), and being slightly flexed at the knee-joint perform a pendulum-like movement (4, 5), the passive foot passing as far in front of the active leg as it was previously behind it. The foot being then placed flat upon the ground, the centre of gravity is



transferred to what now becomes the active leg, the latter being slightly flexed at the knee and placed vertically. The first act is then repeated, and so on. It will be observed that during walking the trunk leans toward the active leg and inclines somewhat forward, the effect of which is to overcome resistance of the air, and that it slightly rotates on the head of the active femur. Running differs from rapid walking in that at a particular moment, both legs not touching the ground, the body is raised in the air, the necessary impetus being given to the body by the forcible extension of the active leg.

## CHAPTER LV.

### REPRODUCTION.

#### SPONTANEOUS GENERATION. FISSIPAROUS, GEMMIPAROUS, AND SEXUAL GENERATION.

At an immensely remote period the earth must have been entirely destitute of life, at least the physical conditions of the azoic period of geologists, and the æons preceding it were such as to make the existence of life, as we are acquainted with it, impossible. Whether the nebular hypothesis of the earth having been cast off from the sun be accepted or not, there can be no doubt that at an inconceivably distant period the earth was in a fluid or semi-fluid molten condition, and its temperature so high as to render life impossible, or even to admit of the union of the chemical elements composing it, the latter existing then separately, as they do in all probability now, in the sun, as shown by spectral analysis. The basalts, porphyries, and lavas entering into the formation of the igneous rocks, the volcanic action constantly going on at the present day in many parts of the world, the seismic disturbances, the high temperature of mines, etc., not only prove that originally the world was but little else than a ball of fire, but also that the fire, far from being extinguished, is only now restricted to the inner subterraneous regions lying under the crust of the earth. If speculation be admitted, we can conceive how with the loss of heat and the lowering of the temperature through the combination of hydrogen and oxygen that water was formed, and that gradually through the combination of the chemical elements the binary and ternary salts entering into the formation of the rocks constituting the crust of the earth were next produced, and, finally, the physical conditions being suitable, that the combination of carbon, hydrogen, oxygen, nitrogen, and phosphorus or sulphur atoms, resulted in the development of protoplasm, or the simplest kind of life. It is true that the idea of life being generated spontaneously, as just supposed, is repugnant to all that we know of life as reproduced at the present day, there being no evidence whatever that life now is ever generated otherwise than from preëxisting life, solitary tapeworms, maggots, etc., often cited by the uneducated as instances of animals spontaneously generated, offering no exception to the rule, being in reality reproduced, like all life, by preëxisting animal life. That the first life appearing upon the face of the earth was nevertheless spontaneously generated, developed independently of preëxisting life must be admitted, since there was no antecedent life during the azoic period to give rise to it. As to the conceivability or inconceivability of how spontaneous generation was brought about, of how protoplasm, with its remarkable properties, was ever developed



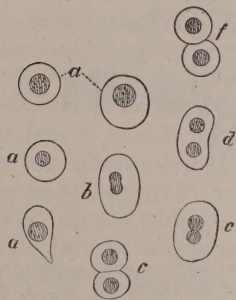
through the combination of chemical elements possessing different properties, it may be said that it is just as difficult to comprehend how the combination of acid and base will give rise to a salt exhibiting properties possessed by neither, or how two gases like oxygen and hydrogen in combination produce a liquid, water, different from either. In either case we must suppose that the properties of the substance formed, however remarkable, are the sum of the properties of the elements entering into combination and giving rise to the substance, whatever is true of the inorganic in this respect being true of the organic as well, the question in either case being one of the redistribution of matter and force only. Admitting that life originated spontaneously, there is little reason, however, to hope that the physical conditions which obtained when life first appeared upon the face of the earth can ever be realized experimentally so as to enable one to generate life *de novo*. Still it must not be forgotten that what appears impossible, inconceivable, to one age, becomes perfectly so to a succeeding one. Life having once appeared upon the face of the earth, however produced, there is no reason to suppose that it has ever been entirely absent, since catastrophies, such as volcanic eruptions, earthquakes, floods, climatic changes, etc., which are so destructive to life, are relatively local in action. Further, the first life, out of which all life has since been gradually developed through inheritance and variation, must have been of the simplest kind; indeed, so simple as to make it difficult, if not impossible, to say whether such life should be regarded as animal or vegetable, its characters being intermediate between, and partaking of the nature of both plants and animals. The latter, judging from their remains as presented in the Cambrian and Silurian rocks, or such as immediately overlie the azoic strata, were also at first of a simple kind. Thus among the plants and animals living in these early ages of the primary period of geologists may be mentioned seaweeds, jelly fish, coral-making polyps, crinoids, brachiopods, various kinds of mollusca, trilobites, etc. Passing on through the later ages of the primary period, the life becomes more varied and complex; fishes, ganoids, and sharks, and land plants, pine-like lepidodendrons, and ferns making their appearance during the Devonian age, or that of the sandstone, and reptiles in the carboniferous age, or that of the coal period, remarkable also for the richness of its cryptogamous plants. As the ages rolled on, during which the Jura rocks were deposited in Switzerland, the chalk cliffs in England, the marls in New Jersey, phanerogamous or flowering plants, palms and trees like those of our own forests, oaks, dogwoods, poplars, beeches, appeared, while among the animals that lived during these ages may be mentioned fishes resembling those of the present day; gigantic reptiles, birds, and probably a few marsupial mammals.

During the tertiary period that followed, the flowering plants and trees then flourishing resembled closely those of the forests of the present day, the invertebrate forms of life differed but little from those existing now, the fishes and reptiles were similar to those found in our rivers, oceans, and forests; while herbivorous animals, resembling the tapir, peccary, camel, deer, horse, rhinoceros, and elephant, roamed in herds

over the continents, hippopotami wallowed in the streams; while beasts of prey were also numerous, being represented by animals closely allied to the lion, tiger, hyena, dog, and panther, of the present day. During the close of the tertiary, or, rather, of the post-tertiary period, the general aspect of the world differed but little from that presented by it now, man appears but in a condition of development, probably far lower than that of the lowest existing savage, and the process of civilization begins.

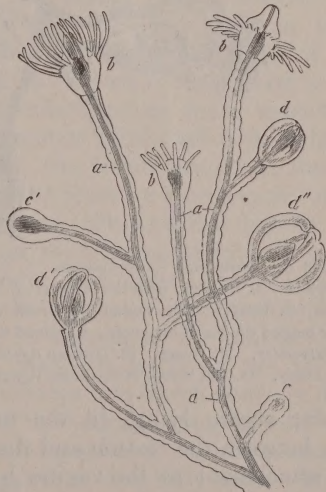
The idea of reproduction is usually associated with that of the difference of sex; the production of offspring naturally suggesting the idea of two parents. Many plants and animals, however, are reproduced entirely independent of sexual intercourse, by what is known as fission or gemmation; and as many of the structures of the body are developed by these processes, it is essential that they should be at least briefly illustrated. By the process of fission is meant the division of the single parent organism into two or more parts, each of which will become a new being, similar in form, inheriting the properties of the parent. Reproduction by the process of fission may be observed in many of the lower cryptogamous plants, and among animals in the infusoria, annelida, etc., illustrations of which have been given. What interests us in this connection, however, as regards fission is, that the segmentation of the vitellus of the egg, the development of the embryonic blood corpuscles (Fig. 539), the proliferation of the cells constituting morbid growths, etc., are accomplished by this process. On the other hand, by gemmation is understood the reproduction of the new being by a process of budding, as seen in ordinary flowering plants, and among

FIG. 539.



Division of blood cells in embryo of stag.  
(FREY.)

FIG. 540.



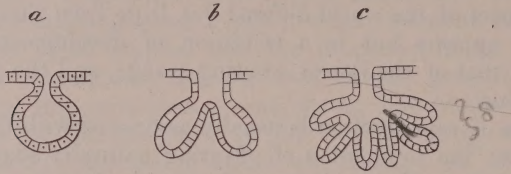
Hydroid colony. *Eudendrium ramosum*.  
(GEGENBAUR.)

animals in the hydra, actinia, etc., each bud becoming a new animal. In certain cases of gemmiparous reproduction, however, the buds, instead of being cast off as produced, remain attached to the parent stock, and so give rise to a colony, as in the hydroids (Fig. 540), each member of which is in communication, directly or indirectly, with each other. Such a mode of reproduction



tion in the human body is seen in the development of a racemose gland (Fig. 541) through the division and subdivision of a simple follicular

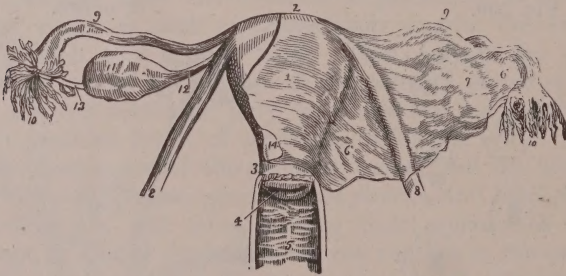
FIG. 541.



Diagrammatic view of development of glands.

gland. The reproduction of man and most animals, however, is accomplished by the union of a spermatozoon and an ovum, specialized products of the male and female generative apparatus respectively, which, while elaborated by a process of fission, or gemmation, unlike the products of the latter, must fuse together in order to give rise to a new being, neither spermatozoon nor ovum, by themselves, being capable of further development. Further, it will be observed that since, in the production of a new being by sexual generation, the union of the spermatozoon and ovum is indispensable, the qualities of the parents must be transmitted to their offspring. The female generative organs, situated partly within and partly without the pelvis, consist of the uterus, Fallopian tubes, vagina, ovaries, the external and internal labia, clitoris, etc. The uterus (Fig. 542), or womb, is a pyriform, hollow

FIG. 542.



Sketch of the uterus and its appendages. 1. Uterus, with its peritoneal covering partially retained. 2. Its fundus. 3. Its neck, with the forepart of the attachment of the vagina removed. 4. Mouth of the uterus. 5. Interior of the vagina. 6. Broad ligament, removed on the opposite side. 7. Position of the ovary behind the broad ligament. 8. Round ligament. 9. Oviduct, or Fallopian tube. 10. Its fimbriated extremity. 11. Ovary. 12. Ovarian ligament. 13. Process connecting the fimbriated extremity with the ovary. 14. Cut border of the broad ligament. (WILSON.)

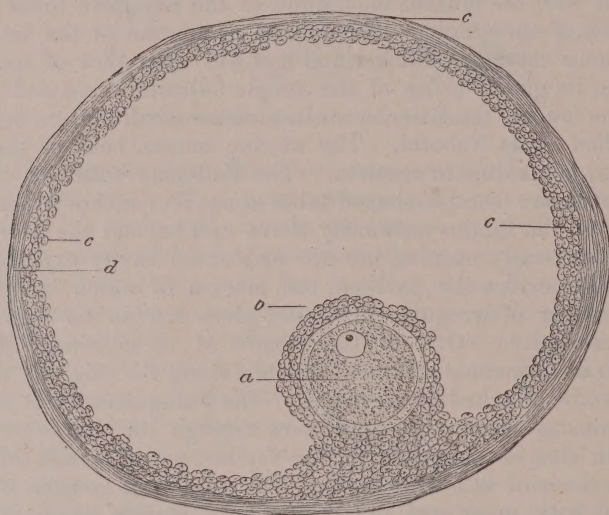
muscular organ, lying, in the unimpregnated condition, within the pelvis, between the rectum and the bladder, and maintained in position by its attachment to the vagina, by the recto- and vesico-uterine peritoneal folds, and the round and broad ligaments, its upper broad extremity is known as the fundus, or base, the narrow extremity the cervix, or neck, and the intervening portion as the corpus, or body. The uterus is about two and a half inches in length, two inches in breadth, and one inch in thickness.

The walls of the uterus consisting of unstriated muscular tissue, being about one-half an inch in thickness, the <sup>its</sup> cavity of the ~~latter~~ is but a narrow space. That of this <sup>the</sup> body is lined with a thin, soft, smooth, and ciliated mucous membrane of a pale red color, containing numerous tubular glands adhering closely to the underlying muscular tissue (the <sup>the</sup> being no intermediate fibrous or submucous tissue) which becomes continuous with the mucous membrane of the Fallopian tubes and that of the neck of the uterus. The mucous membrane of the latter is of the squamous character, thicker and less soft than that of the body of the uterus, its glands being of the simple follicular kind and secreting a tenacious mucus, the latter in an inspissated condition, giving rise to the so-called ovula Nabothi. The uterine mucus, both of the fundus and cervix, is alkaline in reaction. The Fallopian tubes, or the horns of the uterus, are trumpet-shaped tubes about four inches in length, extending from the fundus outwardly above and beyond the ovary. The outer free extremity opening into the abdominal cavity expands into a funnel-shaped orifice the pavilion, the margin of which being fringed with a number of irregular processes, gives rise to its name of fimbriated extremity. One of the largest of these fringed processes, doubled so as to include a furrow, extends along the edge of the broad ligament to be attached to the ovary. The Fallopian tube is lined with ciliated mucous membrane, continuous through its interim or uterine orifice with that of the cavity of the fundus, and disposed in a longitudinal manner or as narrow folds. The tube itself consists of fibrous intermixed with unstriated muscular tissue, loosely invested by peritoneum. The small sac, often absent, attached by a long pedicle close to the fimbriated extremity, is the remains of the duct of Müller of the embryo, as we shall see presently. The vagina is a cylindrical canal about four inches in length and an inch and a quarter in breadth (in the virgin adult), extending from the uterus, the neck of which projects into it, to the vulva. The vagina consists of three coats, an outer fibro-elastic, a middle unstriated muscular, and an inner mucous; the epithelium of the latter is of the squamous kind, and is provided with numerous minute conical papillæ. In the virgin condition, the lower orifice or entrance of the vagina is constricted by a crescentic or zone-like fold of the lining ~~of the~~ membrane, the so-called hymen. The latter is usually obliterated by sexual intercourse, childbirth, etc.; in some instances, however, it is so strong that even impregnation may occur without its being ruptured. Its presence cannot, therefore, be taken as an evidence of virginity, or its absence of the contrary. The inner surface of the anterior and posterior walls of the vagina is roughened by folds, the wart-like eminences into which they are divided more particularly at the entrance of the vagina being known as the carunculæ myrtiformes. While, as just mentioned, the uterine mucus is alkaline in reaction, that of the vagina is decidedly acid. The two ovaries are compressed ovoid bodies, situated behind the broad ligament and enclosed by a pouch of the latter about an inch from the uterus, to which they are attached by the ovarian ligament. The ovary consists of a reddish spongy fibrous stroma, enclosed in a dense fibrous tunic, the tunica albuginea. Within the stroma of the ovary are found



numerous (several thousand) vesicular-like bodies, varying from a microscopic size to the fourth of an inch in diameter, the Graafian follicles or vesicles, so-called after Regnerus de Graaf their discoverer.<sup>1</sup> These vesicles (Fig. 543), which are especially abundant at the peripheral por-

FIG. 543.



Graafian follicle. (HÆCKEL.)

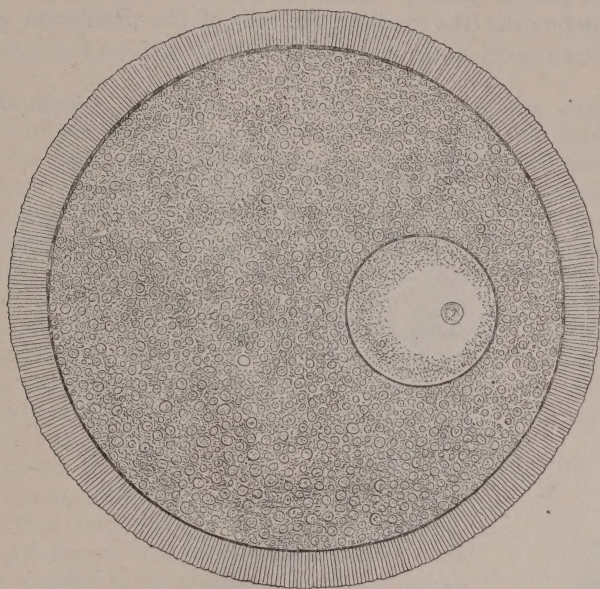
tion of the stroma of the ovary, consist of an outer fibro-vascular layer or tunic, a middle basement membrane or membrana propria, and an inner layer of polyhedral granular epithelial cells, the membrana granulosa. At the side of the Graafian follicle lying next the surface of the ovary, the cells of the membrana granulosa are heaped up, constituting the discus proligerus, within which is found the ovum or egg, only discovered as recently as 1827 by Von Baer.<sup>2</sup> The remaining portion of the Graafian follicle—that is, the part not occupied by the discus proligerus with the enclosed egg—is filled with a serous liquid containing granules, nuclei cells apparently detached from the membrana granulosa. The ovum or egg as just discharged from the follicle, has usually adhering to it the cells of the discus proligerus and shreds of epithelium; the latter being removed, the egg can then be seen with the naked eye on a perfectly clean piece of glass as a very minute speck, averaging in length the  $\frac{1}{120}$ th of an inch ( $\frac{1}{2}$  millimetre) in diameter. Under the microscope the ovum or egg (Fig. 544) appears as a spheroidal body, exhibiting the characters of an organic cell as already described. Thus, it consists of a cell wall, an elastic vitellus membrane, the zona pellucida, measuring about  $\frac{1}{2500}$ th of an inch ( $\frac{1}{100}$ th of a millimetre) in diameter, and which, while apparently a clear pellucid membrane, is in

<sup>1</sup> De Mulierum Organis Generationi inservientibus Tractatus Novus, p. 177. Lugd. Batav., 1672.

<sup>2</sup> De Ovi mammalium et hominis generi, Lipsiæ, 1827. Ueber Entwicklungs Geschichte der Thiere, Königsberg, 1828.

reality striated, the striæ being probably canals through which the spermatozoa pass into the egg.

FIG. 544.



The human ovum. (HECKEL.)

The cell contents, yolk or vitellus, enclosed within the zona pellucida, consist of a soft or semifluid protoplasmic matter, containing granules and oil globules, among which may clearly be seen a nucleus and nucleolus. The nucleus, or germinal vesicle, as it is called, in the ovum discovered in mammals by Coste,<sup>1</sup> in 1834, usually situated near the surface of the egg, is a clear, spheroidal vesicle, and measures about the  $\frac{1}{500}$ th of an inch ( $\frac{1}{2}$ d of a millimetre), containing granular fluid, and the nucleolus, macula, or the germinal spot. The latter, discovered by Wagner,<sup>2</sup> in 1835, measures about the  $\frac{1}{3600}$ th of an inch ( $\frac{1}{4}$ th of a millimetre, in diameter). It is a fact of profound significance that the human ovum, or first cell, from which all the cells composing the body are developed, should be practically undistinguishable, morphologically at least, from the ova of the remaining monodelphous mammalia; and further, that the first or transitory egg-stage through which man passes should be permanently retained as such through life in many of the lower plants or animals, such beings never passing beyond this unicellular stage. Further, the very lowest forms, as well as the highest forms of life, including man, begin in exactly the same way as masses of protoplasm; the immature human ovum, like an immature ova, being a mass of protoplasm and the zona pellucida a secondary formation. The ova are developed from the germinal epithelium (Fig. 545), a

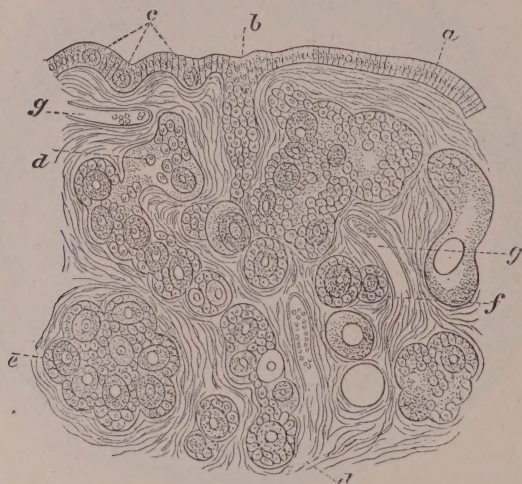
<sup>1</sup> Recherches sur la génération des Mammites par Delpech et Coste, Paris, 1834.

<sup>2</sup> Müller: Archiv, 1835. Prodromus historiae generationis, Lips., 1836.



covering of the primitive ovary. Through the inward growth of this epithelium into the substance of the ovary, cords of cells (*b d*) are formed, which become divided into compartments through the encroachment of the fibrous stroma. Of the cells within these compartments the largest become ova; the smallest, the cells of the membrana granulosa

FIG. 545.



Vertical section through the ovary of a newborn female. (WALDEYER.)

of the Graafian follicle (*e f*), the wall of which is continuous with the stroma. As development advances, fluid accumulates between the growing cells, the follicle assumes the shape of a vesicle, the egg lying eventually to its inner wall. With the ripening or maturation of the ovum, the Graafian follicle comes to the surface of the ovary, the wall of which as well as that of the follicle becoming at the same time thinner and thinner, until, finally, they are ruptured, and so permit of the escape of the egg. From the fact of the egg or embryo being found in the Fallopian tube or uterus, instead of in the abdominal cavity, except in the unusual case of abdominal pregnancy, it is evident that the Fallopian tube must be so disposed with reference to the Graafian follicle that at the moment of its rupture a temporary passage-way is usually formed from one to the other. As a matter of fact, it is not positively known how the egg passes from the Graafian follicle to the Fallopian tube. It may be supposed, however, that the fimbriated extremity affixes itself to the ovary at the moment of rupture of the follicle, or that the egg, dropping into the furrow of the long fimbriated process situated at the edge of the broad ligament and attached to the ovary, is transferred by ciliary action into the orifice of the tube, and thence by the same kind of action through the Fallopian tube into the uterus. The egg having arrived in the cavity of the latter, if not in the meantime impregnated, sooner or later decomposes and disappears. Before describing, however, the manner in which the ovum is impregnated,

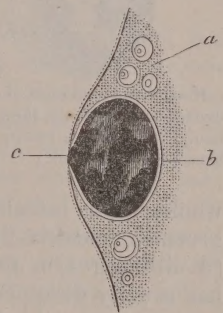
certain changes undergone by the Graafian follicle and the mucous membrane of the uterus, incidental to the maturation and escape of the ovum from the follicle, whether the ovum be impregnated or not, must be first considered.

### CORPUS LUTEUM OF MENSTRUATION AND PREGNANCY.

It is impossible to convey by words any idea of the extent of the congestion of the internal generative apparatus of the female during the period of the maturation and escape of the ovum from the Graafian follicle. The author can only say that in making post-mortem examinations of females dying while menstruating, he was impressed with the fact that the bloodvessels (arteries, capillaries, and veins) were distended to an extent never accomplished by an artificial injection, however successfully performed. Such being the case (as might be expected), with the rupture of the Graafian follicle, there being quite an abundant hemorrhage, the cavity of the follicle fills with blood. The latter soon coagulating, as it would do if extravasated elsewhere, the clot remains enclosed within the walls of the follicle (Fig. 546), having no organic connection, however, with the latter, but simply lying loose in the cavity of the follicle, out of which it can be readily turned by the handle of a scalpel. The clot, which at this moment is large, soft, and gelatinous, soon begins to contract, and the serum exuded being absorbed by the adjacent parts, it becomes smaller and denser. The coloring matter of the clot at the same time undergoing the usual changes incidental to extravasation, and being to a great extent absorbed with the serum, a diminution in its color becomes quite perceptible. During this period, about two weeks, the lining membrane of the follicle, which at the moment of rupture presents a smooth, transparent, vascular appearance, becomes much thickened and convoluted. Through the continued condensation of clot and thickening of the lining membrane, as just described, the follicle has become so altered in its appearance that by the end of three weeks it can be no longer recognized as such, and is henceforth known as the corpus luteum, though its color can scarcely be said as yet to be distinctly yellow. At this period the corpus luteum may be described as a rounded tumor, about four-fifths of an inch (twenty millimetres) in length, situated in the stroma of the ovary, and projecting from the surface of the latter, the surface of the corpus presenting a minute cicatrix, the mark of the rupture of the follicle.

If such a corpus luteum be divided longitudinally (Fig. 547), it will be found to consist of a central clot and a convoluted wall, and it will be observed that, while the clot and the convoluted wall lie in contact with each other, there is neither any organic connection between the convoluted wall and the clot, on the one hand, nor the surrounding ova-

FIG. 546.

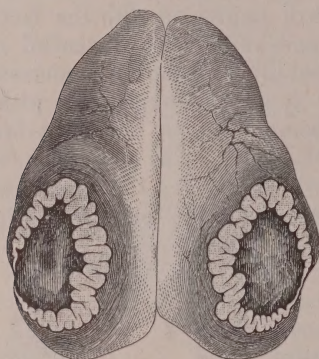


Graafian follicle, recently ruptured during menstruation, and filled with a bloody coagulum; shown in longitudinal section. *a*. Tissue of the ovary. *b*. Membrane of the vesicle. *c*. Point of rupture. (DALTON.)



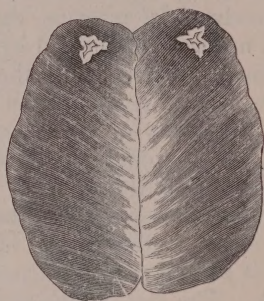
rian tissues, on the other. From this time on, the corpus luteum undergoes a retrograde metamorphosis. By the end of the fourth week it is diminished to about half of the size attained at the end of the third week, the central clot has been, to a great extent, absorbed, the convoluted wall is with difficulty separated from the central clot and the peripheral ovarian tissue, and its color, instead of having faded, like that of the clot, is now of a bright yellow. After this period it will be found impossible to separate the yellowish convoluted wall, either from the ovarian tissue or the central clot, and by the end of two months the

FIG. 547.



Human ovary cut open, showing a corpus luteum, divided longitudinally, three weeks after menstruation. From a girl, twenty years of age, dead of hæmoptysis. (DALTON.)

FIG. 548.



Ovary, showing corpus luteum, nine weeks after menstruation. From a girl dead of tubercular meningitis. (DALTON.)

whole corpus luteum will be found to be reduced to the condition of a greenish, cicatrix-like spot (Fig. 548), about one-fourth of an inch (6 millimetres) in diameter. At the end of six months the corpus luteum has usually disappeared. It may, however, be sometimes found, though in a very atrophied condition, even seven or eight months after the rupture of the follicle. Such, in brief, is the manner in which the corpus luteum of menstruation is developed out of the ruptured Graafian follicle from which the ovum has escaped, at least as observed by the author in a number of females dying from natural causes or violent deaths, and which does not differ essentially from the process so admirably described by Dalton.<sup>1</sup> As during pregnancy far more blood flows to the female generative apparatus than during menstruation, it might necessarily be supposed that while the production of the corpus luteum would be essentially the same in both conditions, the corpus luteum, being better nourished, would grow larger and persist longer than the corpus luteum of menstruation. That such is the case there can be no doubt, a corpus luteum being present at the end of pregnancy even, and measuring as much as half an inch in diameter. While marked differences exist, therefore, between the corpus luteum of menstruation and that of pregnancy, nevertheless, as these differences are

<sup>1</sup> Trans. of the American Med. Assoc., vol. iv. p. 547. Phila., 1851. Physiology, 7th edit., p. 608. Phila., 1882.

of degree, and not of kind, and since the corpus luteum of menstruation during the first three weeks increases in size, but that of pregnancy after the first six months diminishes, it can be readily conceived that at a particular moment the corpus luteum of menstruation might be of the same size as that of pregnancy, and that if the color of the clot and convoluted wall in the two were not well marked, the two corpora lutea might be undistinguishable. At least such has been the experience of the author, in comparing numerous corpora lutea of menstruation of various ages with those of pregnancy. Further, that the presence or absence of a corpus luteum cannot be accepted as positive evidence of impregnation having taken place is shown by the fact that, although in several instances during post-mortem examinations a foetus was removed from the uterus by the author, not a trace of a corpus luteum could be found in either ovary, and, on the other hand, in more than one instance a well-developed corpus luteum being present several months after the last menstruation, there was not the slightest reason to believe that during that period there had been a foetus in the uterus, at least the relatives of the deceased had no object in concealing the fact of impregnation, if such had really occurred.

#### MENSTRUATION.

Coincident with the maturation and escape of the ovum from the Graafian follicle, the mucous membrane of the uterus undergoes several well-marked changes. Thus, while in the ordinary conditions it measures only about the one-fourteenth of an inch in thickness, at this period it becomes twice or even three times as thick. It is also much softer and more loosely attached to the underlying part than ordinary, being somewhat rugose in character. The glands are very much enlarged, and the surface of the membrane smeared with blood. The latter is due to a kind of fatty degeneration set up in the mucous membrane involving the bloodvessels, by which the capillaries are ruptured. The hemorrhage so caused constitutes the menstrual flow, or the menses, catamenia, etc., and appears monthly in the healthy female. It appears to be pure arterial blood mixed with desquamated utero-vaginal epithelium; the amount of the latter would appear from the observations of the author to be greater than usually supposed. The menstrual blood is kept from coagulating by the vaginal mucus. As might be expected from the nature of the case, it is impossible to say how much blood is discharged during the menstrual period, for, apart from the difficulty experienced in collecting it, women vary very much in respect to the amount of blood lost. From five to twenty ounces may be accepted as an approximative estimate of the total flow during the menstrual period. Menstruation is sometimes regarded as the effect of ovulation, the <sup>two</sup> being so intimately associated. Since menstruation, however, occurs without ovulation in the absence of ovaries, and ovulation without menstruation, it is evident that the two phenomena are not related as cause and effect, but should be considered as the effects of a common cause, the general preparation of the system for impregnation. Indeed, the thickening and shedding of the mucous membrane of the uterus, and hemorrhage during menstruation, differ only in degree, not in kind, from the changes



undergone by the mucous membrane during pregnancy and parturition. That the menstrual flow is the effect of a deep-lying cause, the fitting of the mucous membrane for the reception of the ovum, though not due to the production of the latter, is shown by the constitutional disturbance experienced by the female when the menses first appear, and ever afterward with their monthly reappearance, though then to a less extent. The menses usually appear between the age of thirteen and fifteen years and much earlier in warm climates. At this period, the age of puberty, there is a general development of the body, the limbs become fuller and rounder, hair appears on the mons veneris, the mammary glands enlarge, ova mature, and the disposition changes. Just before the establishment of the flow, either in the case of its first appearance or in after recurring ones, for about two days a feeling of general malaise is experienced, particularly a sense of weight and fulness in the pelvic organs, the vaginal mucus is increased in amount and becomes rusty in color, and gives rise to the odor so perceptible in certain females, the breasts also enlarge, showing the sympathies of the latter for the generative organs. With the establishing of the flow, the disagreeable feelings and uneasiness usually pass away, and by the end of the fourth day, though the time varies, the flow ceases, and the mucous membrane returns to its normal condition. At about forty-five years of age the menses become irregular in their recurrence and usually cease altogether at fifty. The phenomenon of the menses is not restricted to the human female, as is often supposed, the heat or rut of the lower animals being essentially the same process. Indeed, in the monkeys (macacus cynocephalus), apes, <sup>there</sup> ~~there~~ is a discharge of blood monthly, and in the mare, cow, and dog the same, but recurring at longer intervals. It is a significant fact, that the females of animals, except monkeys, only receive the male during the rutting or menstruating period.

### THE MALE GENERATIVE APPARATUS.

The male generative apparatus consists of the testicles, the spermatic ducts, the seminal vesicles, prostate and suburethral glands, and the penis. The testicles (Fig. 549), secreting the spermatic fluid, are two glandular bodies suspended by the spermatic cords within the scrotum. The latter is essentially a musculo-cutaneous pouch, divided into two recesses by a septum, for the reception of the two testicles. Each testicle consists of an anterior oval portion of the body or testes proper, and a posterior elongated portion clasping, as it were, the former, the epididymis. The upper portion of the epididymis is known as the head or globus major, the lower part as the tail or globus minor, which in turning upward upon itself, becomes the spermatic duct. The testes are covered with a dense white fibrous membrane, the tunica albuginea, which at the back of the testes forms a process, the mediastinum. The latter being prolonged as fibrous bands to be inserted into the inner surface of the tunica albuginea, serves as a sort of scaffolding to support the delicate glandular substance within. The testicle proper, is made up of about two hundred lobules, each lobule in turn consisting of from one to six seminiferous tubules, of which there are perhaps eight hundred in all.

The seminiferous tubules at the narrow end of the lobule assume a straight course, being then known as the vasa recta. The latter entering the mediastinum, constitute together the plexus retiformis, from which emerge about a dozen efferent canals, or vasa efferentia, to pass out to the head of the epididymis. Within the latter these

FIG. 549.



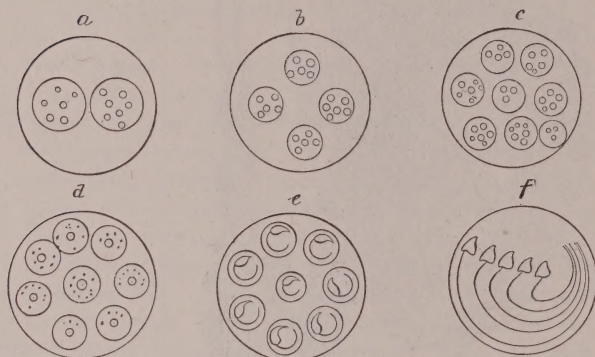
Testicle and epididymis of the human subject. *a.* Testicle. *b.* Lobules of the testicle. *c.* Vasa recta. *d.* Rete testis. *e.* Vasa efferentia. *f.* Cones of the globulus major of the epididymis. *g.* Epididymis. *h.* Vas deferens. *i.* Vas aberrans. *m.* Branches of the spermatic artery to the testicle and epididymis. *n.* Ramification of the artery upon the testicle and epididymis. *o.* Deferential artery. *p.* Anastomosis of the deferential with the spermatic artery. (KÖLLIKER, *Handbuch der Gewebelehre*, Leipzig, 1867, S. 523.)

efferent canals form the spermatic cones, which finally give rise to one convoluted tube, constituting the body and tail of the epididymis, the latter of which, as just mentioned, becomes the spermatic duct. The spermatic duct passing through the inguinal canal, leaves the latter at the internal abdominal ring, and descending backward and downward, passes forward to form, together with the duct of the seminal vesicle, the ejaculatory duct, the latter terminating in the prostatic urethra. The seminiferous tubules, about thirty inches in length when unravelled, and the  $\frac{1}{120}$ th of an inch in diameter, consist of a fibro-membranous wall lined with a delicate layer of soft polyhedral nucleated cells, the sperm cells, which elaborate the spermatic or seminal liquid, of which about half a drachm is emitted during the orgasm. The latter is a faintly alkaline liquid, slightly heavier than water, becoming jelly-like first, and then hardening after emission. Of a thousand parts, perhaps one hundred are solid. Chemically but little is positively known of its composition; phosphates appear, however, always to



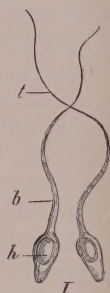
be present, notably magnesium phosphate. Physiologically the essential portion of the spermatic fluid, upon which its fecundating powers without doubt depend, are the spermatozoa that it contains. Indeed, if the seminal liquid be deprived of its spermatozoa, it is rendered entirely inoperative as regards impregnation. Of the sperm cells just mentioned, which elaborate the sperm, some are larger than others, and it would appear that the development of the spermatozoa appearing first at the age of puberty and afterward up to ninety years of age, and longer, takes place only within these larger cells, the granular nuclei of which divide (Fig. 550) and subdivide, one of the nucleoli of each

FIG. 550.



Diagrammatic view of development of spermatozoa.

FIG. 551.

Spermatozoa of man. *h*, apparent nucleus. *b*, body. *t*, tail.

nucleus assuming the form of a spermatozoon, which is set free by the deliquescence of the cell wall enclosing it. The spermatozoa (Fig. 551), discovered by Hammins or Von Hammen in 1677, and described by Leeuwenhoek, resemble the flagellate animalculæ for which they were first taken. A spermatozoon consists of an ovoidal head, apparently containing a nucleus, about the  $\frac{1}{50000}$ th of an inch in length, and of a filamentary appendage or tail the  $\frac{1}{5000}$ th of an inch in length, which vibrates with astonishing rapidity. The movements of the spermatozoa are arrested by water and cold, retarded by acids, and favored by alkalis. The spermatic fluid, with the spermatozoa, passes from the testicles by the spermatic ducts to the seminal vesicles, where it becomes mixed with the secretion of the latter, the nature and use of which are, however, doubtful, as no secreting glands are found in these vesicles; its use may be to dilute the mixed spermatic fluid. The spermatic fluid having accumulated in the seminal vesicles is thence introduced during coition, still further mixed with the secretion of the prostate gland, of the glands of Cowper, and of the urethra, the use of which is not known, by an ejaculatory effort, into the vagina of the female, the spermatozoa by their vibrating movements passing up into the Fallopian tubes, and even the ovaries, as shown by the development of the ovum in those situations in cases of extra-uterine pregnancy. In order that coition should be accomplished, it is essential that the

penis should be erect. This is brought about through its blood supply being very much increased by the stimulation of the vaso-dilator fibres of the nervi-erigentes, the latter arising probably from the second sacral nerves. The centre of erection, situated in the cord, can be reflexly stimulated either by impressions made upon the genital organs, or upon the mind. The ejaculatory effort is due to the simultaneous contraction of the bulbo-urethræ, ischio-cavernous, and transverse perinæus muscles, due to the reflex stimulation of the ejaculatory centre of the spinal cord, situated in the lumbar region.



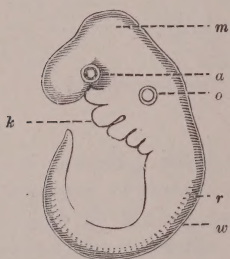
## CHAPTER LVI.

### REPRODUCTION.—(*Concluded.*)

#### IMPREGNATION OF THE OVUM AND DEVELOPMENT OF EMBRYO.

As a matter of fact, nothing is known as to the manner in which the ovum is impregnated in the human female, or of the early stages of the development of the embryo. Since the primitive ova of all animals are, however, alike, and the mature eggs of ordinary mammals undistinguishable from that of the human female, and as the spermatozoa of the mammalia and animals generally differ from each other unessentially, it is to be inferred that the process of impregnation in the human female is the same as that observed in animals. Further, as the human foetus of about three weeks old (Fig. 552) differs but little from that of the rabbit at about

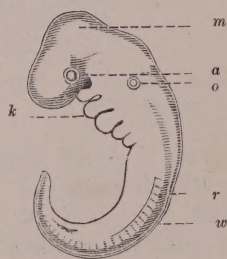
FIG. 552.



Embryo of man.

a. Eye. m. Mid-brain. o. Ear. r. Spinal marrow. w. Vertebral column. k. Visceral arches. (HÆCKEL)

FIG. 553.



Embryo of rabbit.

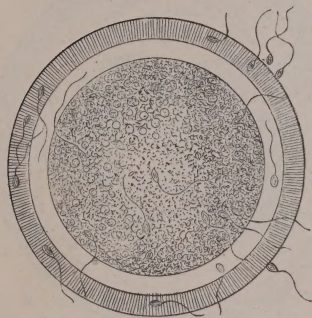
ten days (Fig. 553), there can be little doubt that the stages intermediate between that of the egg and that of three weeks old, through which the human embryo passes, are essentially the same as the corresponding stages through which the rabbit embryo passes from the stage of the egg to that represented in Fig. 553, or the corresponding stages in the development of the dog, hog, etc., or even bird, reptile, or fish. Assuming, then, that the development of man, in the early stages, is the same as that of a rabbit, for example, we will describe, as illustrating the former, the development of that animal, as based principally upon the researches of Bischoff<sup>1</sup> and Van Beneden,<sup>2</sup> up to the period that it begins to differ from man. The act of impregnation in the rabbit, and in all animals in which impregnation has been observed, consists in the passage of one or more spermatozoa (Fig. 554) through the vitelline membrane of the egg

<sup>1</sup> Entwicklungs Geschichte des Kaninchen-Eies, Braunschweig, 1842.

<sup>2</sup> La maturation de l'œuf, etc., d'après des recherches faites chez le lapin, Bruxelles 1875

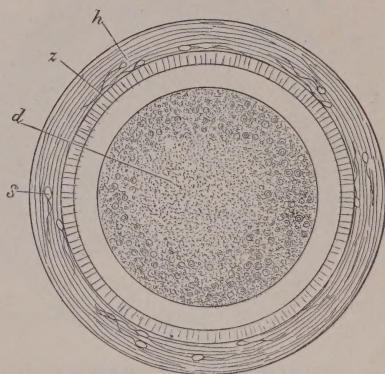
into the vitellus, the germinal vesicle in consequence immediately disappearing. The first effect of fecundation appears, then, to be the reducing of the distinctly nucleated egg to the condition of a monera-like ball of protoplasm (Fig. 555), hence the name of monerula, given by Hæckel, to this, the first stage of the development of the embryo. It will be

FIG. 554.



Passage of spermatozoa into vitellus.  
(HÆCKEL.)

FIG. 555.



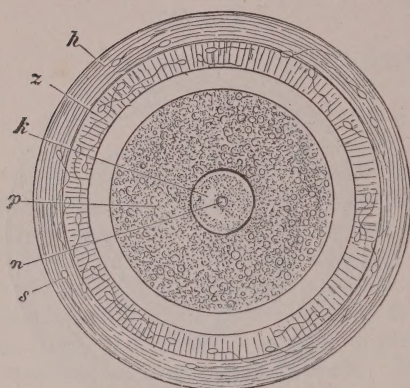
Monerula of rabbit. (HÆCKEL.)

observed, also, that the inner yolk (*d*), or protoplasm, has receded somewhat from the cell-wall or zona pellucida (*z*), and that the latter is covered with several concentric layers (*h*) of an albuminous nature deposited during the passage of the egg through the Fallopian tube. The egg, after fecundation, does not remain in this unnucleated condition long, a new nucleus and nucleolus appearing. The latter has, however, an entirely different morphological significance from the germinal vesicle and spot of the primitive or unimpregnated egg, being developed, in all probability, by the fusion or coalescence of the head of the spermatozoa or pronucleus with the remains of the germinal vesicle, probably the nucleolus or female pronucleolus, the latter coming to the surface of the ovum, as it were, to meet the spermatozoan. While there is no doubt that the new nucleus and nucleolus are due to the fusion in some way of the spermatozoön with the old germinal vesicle, or part of the same, the exact details of the process not having yet been worked out, at least satisfactorily, we will not dwell further upon it. It may also be added that though one spermatozoön only appears to enter into the formation of the new nucleus, and suffices, therefore, for fecundation, there can be no doubt that numerous spermatozoa pass into the vitellus during the act of impregnation. The author has observed this too often in the ova of the lower forms of life, as well as in some of the higher, to have any doubt himself as to the fact, whatever its significance may be. With the appearance of this new nucleus and nucleolus (*n*, Fig. 556), the egg passes from the first or monerula stage to that of the cytula stage, as it is called by Hæckel, or parent cell stage, from the fact of its being the parent of all the future cells of which we have seen the tissues of the body consist. Shortly after the appearance of the nucleus and nucleolus the process of



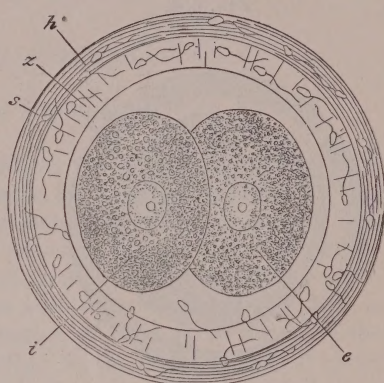
the cleavage, segmentation, or furrowing of the vitellus begins—that is, the vitellus subdivides into two spheres, each of which is provided with a nucleus and nucleolus (Fig. 557). The two spheres, so formed by fission, subdividing into four (Fig. 558), and the four into eight, the

FIG. 556.



Cytula of rabbit. (HÆCKEL.)

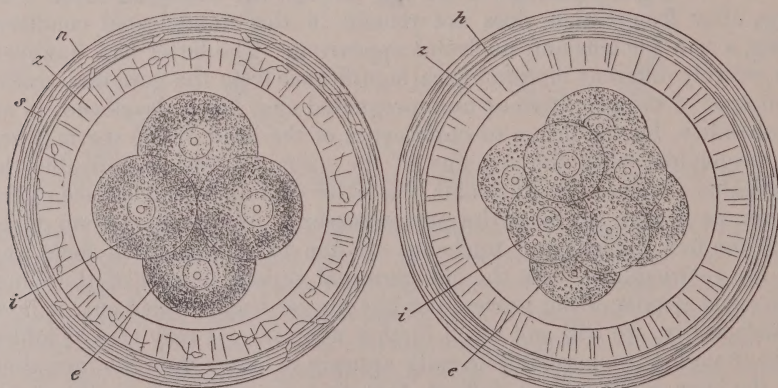
FIG. 557.



Segmentation of vitellus in rabbit (HÆCKEL.)

eight into sixteen, and so on, the original single vitellus becomes finally transformed into a mulberry-like mass of vitelline spheres, the vitelline membrane remaining, however, undivided. These cells are not of the same size and are differently affected by reagents. The larger cells

FIG. 558.

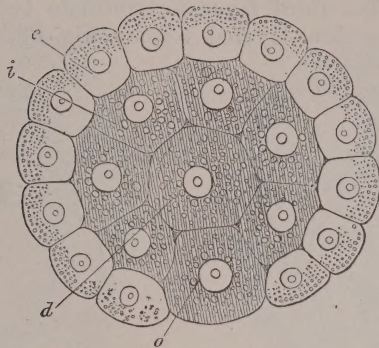


Segmentation of vitellus in rabbit continued. (HÆCKEL.)

originally, the smaller ones finally, arrange themselves in the centre, the smaller ones at the periphery and in a single row, the latter enclosing the former, as a cup, its contents. The egg now reaches its gastrula stage (Fig. 559). Shortly afterward, however, through one of the larger inner cells being drawn inward the mouth (*o*) of the gastrula disappears, and the latter now forms a ball consisting of larger cells within and covered by a single layer of small vesicles without. Fluid, formed probably through the deliquescence of some of the cells, appears between the inner

cells and the layer of outer ones; the latter is expanded into a one-layered globular vesicle, the inner cells remaining as a ball of cells adhering to the outer layer at the point where the mouth of the gastrula was situated. The inner cells now lose their ball-like form, and becoming flattened,

FIG. 559.



Gastrula of rabbit, in longitudinal section. (HECKEL.)

assume a discoidal shape, spreading themselves out. The gastrula, so modified, is now known as the blastodermic vesicle (Fig. 560), and consists, as shown in section, of the original zona pellucida or cell-wall (*a*) which we shall henceforth designate as the chorion, of a single layer of

FIG. 560.

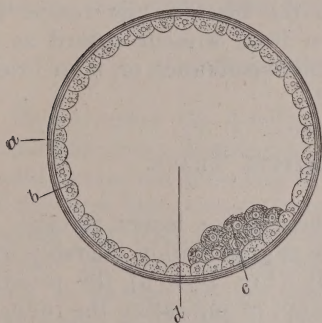
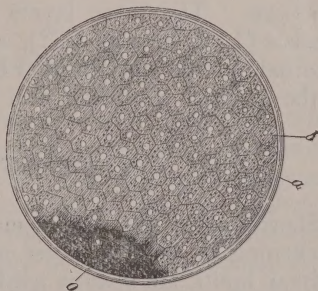
Blastodermic vesicle of rabbit seen in section.  
(HECKEL.)

FIG. 561.

Blastodermic vesicle of rabbit, seen from surface.  
(KÖLLIKER, after BISCHOFF.)

cells (*b*) lying next to the chorion and constituting the wall of the blastodermic vesicle, of a heap of cells (*c*) adhering to the inner surface of the wall. The latter being darker in color than the cells forming the wall of the vesicle, looks like a dark mass when the blastodermic vesicle is viewed from the surface, the cells of the wall then appearing like a mosaic (Fig. 561).

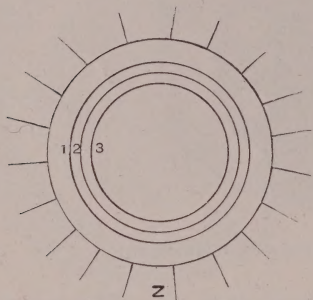
The changes just described by which the egg is transformed into the blastodermic vesicle appear to take place as the egg passes through the Fallopian tube.



## FORMATION OF BLASTODERMIC MEMBRANE.

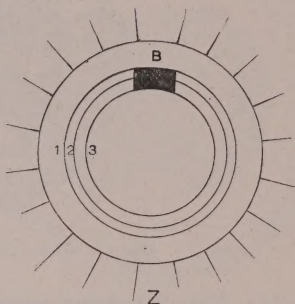
The blastodermic vesicle does not remain, however, long a one-layered vesicle, but soon, through the extension of the disk-like dark cells around to the opposite pole of the egg, a two-layered vesicle; and further, through the development of a third layer intermediate between the external and internal one, a three-layered vesicle (Fig. 562), not including, of

Fig. 562.



Diagrammatic view of ovum of rabbit, consisting of chorion, enclosing three-layered blastodermic vesicle.

Fig. 563.



Diagrammatic view of ovum of rabbit to show formation of primitive trace (B) by fusion of blastodermic membrane.

course, the chorion (Z) or the original zona pellucida of the egg, which now presents here and there over its outer surface little wart-like villous processes. The three layers of which the blastodermic vesicle now consists (1, 2, 3, Fig. 562), are known from without inward as the external, middle, and internal blastodermic membranes, or, more briefly as the epiblast, mesoblast, and hypoblast.

## DEVELOPMENT OF PRIMITIVE TRACE.

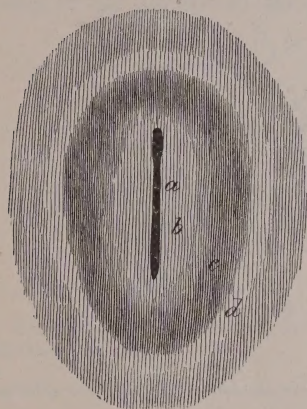
Shortly after the development of these three layers through the thickening of the two outer ones, there appears within tolerably well-defined limits an opaque oval-like body (Fig. 564, *b*), the primitive trace<sup>1</sup> or double shield,<sup>2</sup> so called on account of indicating the rudiment of the body of the future embryo, the remaining portions of the blastodermic membranes not entering into the formation of the body of the embryo, but appropriated, as we shall see presently, to the formation of the true and false amniotic folds and umbilical vesicle. If the blastodermic vesicle be viewed, not in section, but from the surface, the primitive trace will be seen (Fig. 564, *b*) as an oval-like structure, lying in the centre of a pellucid area (*c*), so called on account of the latter being surrounded by an opaque area (*d*), the whole area extending from edge to edge of the area opaca (*d*), being known as the area germinativa, which at this period, while oval-shaped, is at its first appearance

<sup>1</sup> Von Baer : *Über Entwickelungs Geschichte der Thiere, Zweiter Theil*, S. 69, S. 190, Königsberg, 1837.

<sup>2</sup> Remak : *Untersuchungen über die entwickelung der Wirbelthiere*, S. 7. Berlin, 1855.

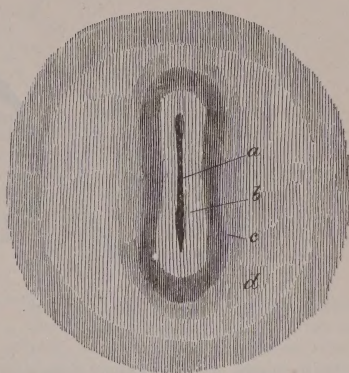
round in form. The opacity of the outer portion of the area germinativa, giving rise to the name of area opaca, is due to the development within the cells of this part of the area germinativa of dark protoplasmic granules. If viewed by reflected light, however, as in Figs. 564 and 565,

FIG. 564.



Primitive trace of rabbit (*b*). Primitive groove (*a*). Area pellucida (*c*). Area opaca (*d*). (HÆCKEL.)

FIG. 565.



Lyre-shaped primitive trace of rabbit. Letters as in Fig. 564. (HÆCKEL.)

the area opaca (*d*) will appear light, and the inner portion of the area germinativa, or the area pellucida (*c*), dark, by comparison the dark ground being visible from below.

#### DEVELOPMENT OF PRIMITIVE ORGANS.

Shortly after the development of the primitive trace (Fig. 564, *b*) within the area pellucida (*c*), there appears along its central line a delicate white streak, the primitive streak<sup>1</sup> or axis plate,<sup>2</sup> due to the coalescence of the three blastodermic membranes along the middle line, as shown by section (Fig. 563, B), and with further developments within the latter a delicate groove or furrow (*a*), which may be called the spinal furrow, since, as we shall see in a moment, through its conversion by deepening and closing into a tube, it gives rise to the spinal cord. As this primitive groove (*a*) deepens, the primitive trace (*b*) and area pellucida (*c*) lose their oval shape and become lyre- or sole-shaped (Fig. 565); the area opaca (*d*), however, reassumes its original round shape. Returning now to the consideration of the embryo as studied by transverse section (Fig. 563), it will be seen from a comparison of the section (Fig. 566) made through an embryo more advanced in development than that of Fig. 604, that not only the primitive groove or furrow (*mr*) is much deepened, but that the external blastodermic membrane rises up into folds (*1a*), which arching over the dorsal surface of the embryo, coalesce in the middle line and form the amnion, the remaining portion of the external

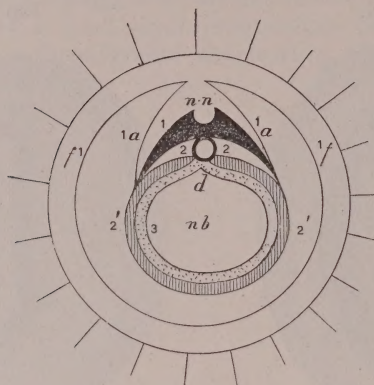
<sup>1</sup> Von Baer, op. cit., Erster Theil. S. 12.

<sup>2</sup> Remak, op. cit., S. 7.



blastodermic membrane receding from the amnion proper as the false amniotic folds ( $f'$ ), until they finally fuse with the inner surface of the chorion (Fig. 566). It will also be observed that the middle blasto-

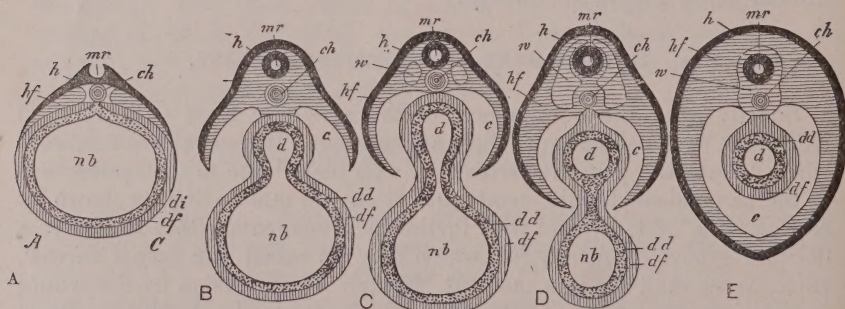
FIG. 566.



Diagrammatic view of ovum of rabbit to show primitive furrow, amniotic folds, splitting of mesoblast.

dermic membrane or mesoblast has split into two layers (Fig. 566, 2, 2'), of which layer 2, or the skin fibrous layer, unites with that part of the external blastodermic membrane, or the skin sensory layer, out of which

FIG. 567.

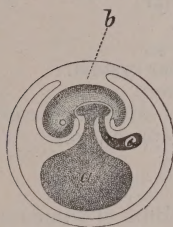


In all the figures the letters indicate the same parts. *h*. Skin sensory layer. *mr*. Spinal tube. *hf*. Skin fibrous layer. *w*. Primitive vertebrae. *ch*. Notochord. *c*. Body-cavity (*cœloma*). *df*. Intestinal fibrous layer. *dd*. Intestinal glandular layer. *d*. Intestinal cavity. *nb*. Navel vesicle. (HECKEL.)

the primitive spinal tube is developed to form the parietes of the body, as shown in Fig. 567 (A, E), representing in section the embryo successively advanced in development, while layer 2', or the intestinal fibrous layer, in adhering to the internal blastodermic membrane, or layer 3, forms the fibro-muscular wall of the primitive alimentary canal and umbilical vesicle (3), the internal blastodermic membrane, or the intestinal glandular layer, giving rise only to the mucous membrane lining the same. An inspection of these different sections will show also, that just as the primitive neural canal, or spinal cord, is developed through the

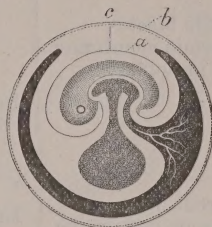
primitive groove (*mr*) being transformed into a tube, which later becomes entirely separated from the external blastodermic membrane, the latter giving rise to the epithelium or epidermis of the skin, so through the deepening of the furrow (*d*) in the internal blastodermic membrane the primitive alimentary canal is formed, the umbilical vesicle, originally part of the same, being constricted off by the bending downward and inward of the parietes of the body.

FIG. 568.



*a.* Umbilical vesicle. *b.* Amniotic cavity.  
*c.* Allantois. (DALTON.)

FIG. 569.



Fecundated egg, with allantois nearly complete.  
*a.* Inner lamina of amniotic fold. *b.* Outer lamina of ditto. *c.* Point where the amniotic folds come in contact. The allantois is seen penetrating between the inner and outer laminae of the amniotic folds. (DALTON.)

An inspection of Figs. 566 and 567 will also show that as the primitive furrow (*mr*) of the external blastodermic membrane is formed there is developed within the middle blastodermic membrane a rod of cartilage (*ch*), the notochord, or chorda dorsalis, which represents the axis around which will be developed the bodies of the future vertebræ, the neural canal being finally enclosed by a bony spinal canal, through ossification of that portion of the mesoblast lying above and on either side of the notochord. The embryo of the rabbit consists at this period, then, apart from the enveloping chorion (Fig. 567, *E*), of two tubes, a neural one above, an alimentary tube below, separated by a rod of cartilage, and enclosed by the walls of the body, the space between the two layers of the mesoblast representing the future body cavity. Resuming what we have just endeavored to describe, it will be seen that through the process of segmentation the vitellus is transformed into a mass of cells, that these cells dispose themselves as three membranes or layers, that the three layers give rise to the primitive organs of the body, out of which the remaining organs are developed, as shown in Table LXXXIII.



TABLE LXXXIII.—MEMBRANES AND LAYERS OF EMBRYO AND ORGANS DEVELOPED FROM THEM.

| Membranes.                                   | Layers.                 | Organs.                                                                                  |
|----------------------------------------------|-------------------------|------------------------------------------------------------------------------------------|
| External blastodermic membrane or epiblast,  | { Skin, sensory,        | { Epidermis.<br>Central nervous system.<br>Primitive kidneys.                            |
| Middle blastodermic membrane or mesoblast,   | { Skin, sensory,        | { Dermis.<br>Peripheral nervous system.<br>Osseous " "<br>Muscular " "<br>Testes.        |
|                                              | { Intestinal fibrous,   | { Vascular system.<br>Mesentery.<br>Wall of alimentary canal and appendages.<br>Ovaries. |
| Internal blastodermic membrane or hypoblast, | { Intestinal glandular, | { Epithelium of alimentary canal and appendages.                                         |

## DEVELOPMENT OF AMNION, ALLANTOIS, AND UMBILICAL VESICLE.

It has already been mentioned that that portion of the external blastodermic membrane not entering into the formation of the embryo, rises up into folds (Fig. 569) at the sides, head, and tail ends of the latter, and arching over its back, and coalescing in the middle line, forms the amnion (*a*), the remaining

FIG. 570.

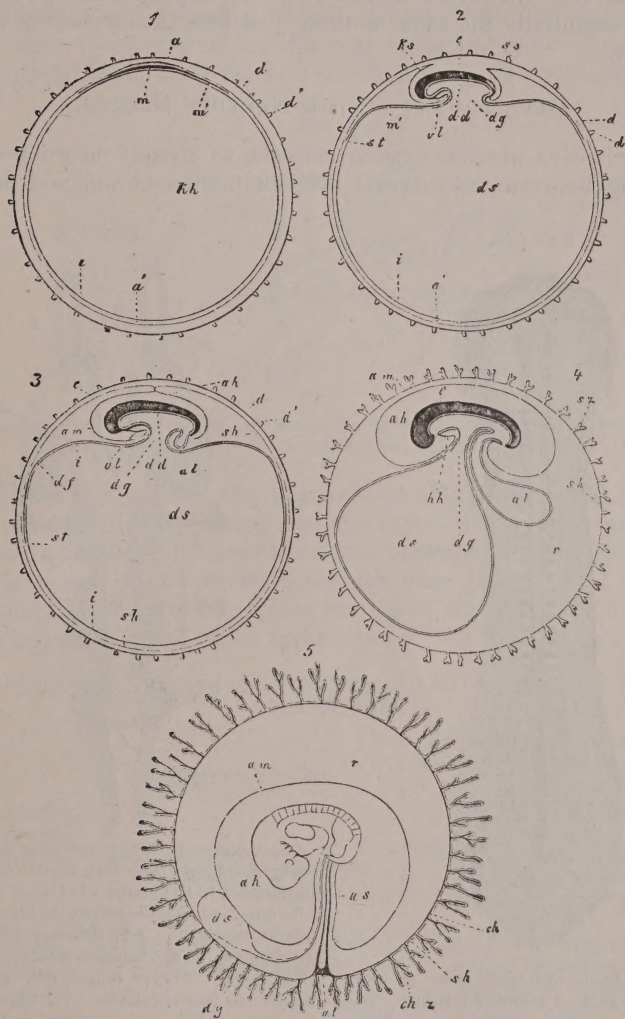


Fecundated egg, with allantois fully formed. *a*, Umbilical vesicle. *b*, Amnion. *c*, Allantois (DALTON.)

peripheral portions of the extensive blastodermic membranes not giving rise to the amnion receding as the false amnion (*b*) from the true one, until it reaches the inner surface of the chorion, with which it ultimately fuses. It will also be observed from Figs. 570 and 571, representing the progressive development of the embryo still further advanced, that during the formation of the amnion (*b*) there buds out as an outgrowth of the posterior portion of the intestine a vesicle, the allantois (Fig. 568, *c*), which, growing outward, gradually extends itself around the entire inner surface of the chorion, the cavity of the vesicle being finally obliterated by the fusion of its outer and inner layers. The chorion, covered with villous processes (Fig. 571, *t*) at this stage will consist, then, from without inward, of the original zona pellucida, of the false amnion, the allantois. As the allantois develops, bloodvessels make their appearance in it, derived from the vessels of the foetus, as we shall see presently, which, in extending into the villous processes of the chorion, serve to convey to the foetus the nutritive material introduced by osmosis from the uterine blood of the mother, the allantois constituting, in fact, the foetal part of the placenta. With the establishing of the allantois, and the consequent nourishing of the foetus by the mother, the umbilical vesicle (Fig. 571, *d s*), which, up to this time, through its vessels,

nourished the same, begins now to diminish in size, and finally disappears altogether. As the human embryo, at the earliest period of its

FIG. 571.



Diagrammatic figures, illustrating the development of the mammalian embryo and the foetal membrane. 1. The blastodermic vesicle invested in the zona pellucida, and showing at its upper pole the embryonic area. 2. Shows the pinching off the embryo from the yolk-sac, and the formation of the amnion. 3. Further development of amnion, and commencement of allantois. 4. Completion of amnion, and growth of allantois. The false amnion, or subgonal membrane, gives off villous processes. 5. The allantois has grown all round the vesicle, and gives off processes into the villi which are much larger than before. The yolk-sac is greatly reduced in size. *a*. Epiblast of embryo. *a'*. Epiblast of non-embryonic part of blastodermic vesicle. *al* Allantois. *am*. Amnion. *ch*. Chorion. *ch 2*. Chorionic villi. *d*. Zona pellucida. *d'*. Processes of zona. *dd*. Embryonic hypoblast. *df* Area vasculosus. *dg* Yolk-stalk. *ds*. Yolk-sac. *e*. Embryo. *hh* Pericardial cavity. *i*. Non-embryonic hypoblast. *kh*. Cavity of blastodermic vesicle. *ks*. Head-fold of amnion. *m*. Embryonic mesoblast. *n*. Non-embryonic mesoblast. *r*. Space between true and false amnion. *sh*. False amnion, or subgonal membranes. *ss*. Veil-fold of amnion. *st*. Sinus terminalis. *si*. Processes of zona pellucida. *vl*. Ventral body-wall of embryo. (KÜLLIKER.)

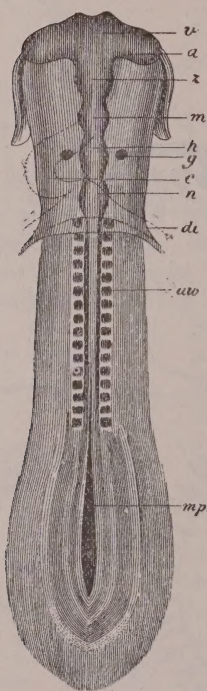


existence, as observed by the author, and by others—that is, from about twelve to fourteen days old—consists, essentially, of the same primitive organs and appendages as that of the rabbit, there can be no doubt that the still earlier stages of its development, not yet actually seen, are essentially the same as those just described as taking place in the rabbit.

### DEVELOPMENT OF THE NERVOUS SYSTEM.

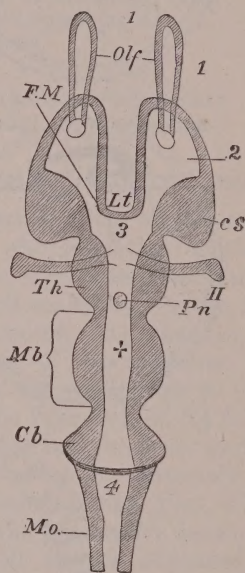
The primitive nervous system consists, as already mentioned, of a tube lying between the external blastodermic membrane and the noto-

FIG. 572.



Primitive brain and spinal tube of man, with sixteen pairs of primitive vertebrae. The brain has parted into five bladders. *v*. Fore-brain. *z*. Twist-brain. *m*. Mid-brain. *h*. Hind-brain. *n*. After-brain. *a*. Eye-bladders. *g*. Ear-vesicles. *c*. Heart. *dv*. Yolk-veins. *mp*. Medullary plates. *uw*. Primitive vertebrae. (HÆCKEL.)

FIG. 573.

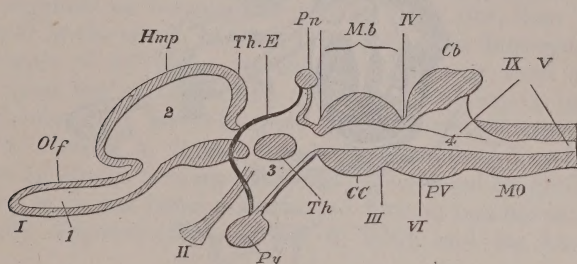


Diagrammatic horizontal section of a vertebrate brain. The figures serve both for this and the next diagram. *Mb*. Mid-brain: what lies in front of this is the fore-, and what lies behind, the hind-brain. *Lt*. Lamina terminalis. *Ol*. Olfactory lobes. *Hmp*. Hemispheres. *Th*. Thalamencephalon. *Pn*. Pineal gland. *Py*. Pituitary body. *FM*. Foramen of Monro. *cs*. Corpus striatum. *Th*. Optic thalamus. *CC*. Crura cerebri: the mass lying above the canal represents the corpora quadrigemina. *Cb*. Cerebellum. *I-IX*. The nine pairs of cranial nerves. 1. Olfactory ventricle. 2. Lateral ventricle. 3. Third ventricle. 4. Fourth ventricle. + Itera tertio ad quartum ventriculum. (HUXLEY.)

chord, and running from one end of the body to the other. As development advances, however, the anterior portion of the primitive neural tube separates, and subdivides into three vesicles: the anterior, middle, and posterior cerebral vesicles; while, through the further subdivision of the anterior vesicle into two, and of the posterior vesicle into two

also, soon five vesicles are developed (Fig. 572), which are known, from before backward, as the prosencephalon, thalamencephalon, mesencephalon, epencephalon, and metencephalon, or as the fore-brain, between brain, mid-brain, hind-brain, and after-brain. In the sending out, anteriorly and laterally, of two vesicles (Figs. 573 and 574) from the anterior vesicle the future olfactory bulbs and optic cups now make their appearance; while through the thickening and inward growth of

FIG. 574.



Longitudinal and vertical diagrammatic section of a vertebrate brain. Letters as before. Lamina terminalis is represented by the strong black line joining Pa and Pg. (HUXLEY.)

the walls of the vesicles, the hemispheres and the ganglia of the brain are developed, the intervening passage-ways—that is, the remnant of the cavities of the original cerebral vesicles becoming from before backward the lateral and third ventricles, the way from the third to the fourth ventricle, the cavity of the spinal portion of the primitive neural tube, persisting as the canal of the spinal cord of the adult.

TABLE LXXXIV.—CEREBRAL VESICLES AND PARTS OF BRAIN DEVELOPED OUT OF THEM.

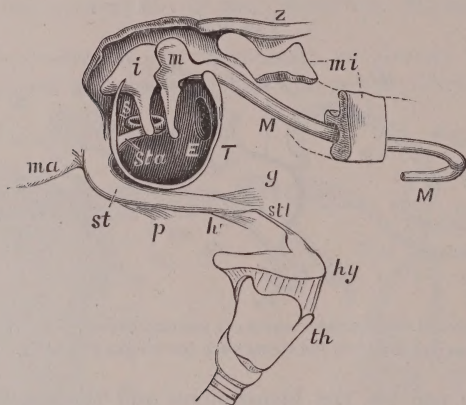
|                                         |   |                                         |                                                                                                                         |
|-----------------------------------------|---|-----------------------------------------|-------------------------------------------------------------------------------------------------------------------------|
| I. Anterior,<br>Primary,<br>Vesicle,    | { | 1. Prosencephalon.                      | { Cerebral hemispheres, corpora striata, corpus callosum, fornix, lateral ventricles, olfactory bulb (Rhinnencephalon). |
|                                         |   | 2. Thalamencephalon,<br>(Diencephalon.) | { Thalami optici, Pineal gland, pituitary body, third ventricle, optic nerve (primarily).                               |
| II. Middle,<br>Primary,<br>Vesicle,     | { | 3. Mesencephalon,                       | { Corpora quadrigemina, crura cerebri, aqueduct of Sylvius, optic nerve (secondarily).                                  |
| III. Posterior,<br>Primary,<br>Vesicle, | { | 4. Epencephalon,                        | { Cerebellum, pons Varolii, anterior part of fourth ventricle.                                                          |
|                                         |   | 5. Metencephalon,                       | { Medulla oblongata, fourth ventricle, auditory nerve.                                                                  |

The primary cerebral vesicles with the secondary parts of the brain developed out of them, may be seen synoptically arranged in Table LXXXIV. At an early period of development these five different parts of the brain may be more or less seen through the membranous head of the embryo (Figs. 552 and 574). Just as we have seen, however,



that through ossification of the mesoblast around and above the chorda dorsalis, the primitive spinal neural canal becomes enclosed in a bony one, the spinal column, so through the ossification of the mesoblast forming the primordial cranium surrounding the primitive cerebral vesicles, the latter, or the future brain, comes to be enclosed in a bony

FIG. 575.



*z.* The zygomatic arch. *ma.* The mastoid process. *mi.* Portions of the lower jaw. *M.* The cartilage of Meckel of the right side, and a small part of that of the left side, joining the left cartilage at the symphysis. *T.* The tympanic ring. *m.* The malleus. *i.* The incus. *s.* The stapes. *sta.* The stapedius muscle. *st.* The styloid process. *p, h, g.* The stylo-pharyngeus, stylo-hyoid, and stylo-glossus muscles. *stl.* stylo-hyoid ligament attached to the lesser cornu of the hyoid bone. *hy.* The hyoid bone. *th.* Thyroid cartilage.

cavity, the skull. There are three marked differences though, to be noticed in the development of the skull as compared with that of the spinal column. First, the notochord does not extend entirely through the head end of the embryo, but stops short in a tapering point at the pituitary fossa. Second, the mesoblast does not split into skin fibrous and intestinal fibrous layers. Third, the primordial cranium never exhibits any trace of segmentation into segments or vertebræ. That the embryo skull does, nevertheless, consist of segments of modified vertebræ, though not in the adult in the sense held by Goethe,<sup>1</sup> the presence of visceral or branchial arches (Figs. 552 and 575) clearly proves, since the latter are morphologically cranial ribs bearing the same relation to different parts of the skull that the thoracic ribs bear to the vertebræ to which they are attached. As the primordial cranium of man, however, shows no trace of such segmentation, gives no evidence of having ever consisted of vertebræ, it is evident that the fusion or coalescence of the same must have taken place at such an early period in the development of the vertebral type that no trace of the primitive segmentation of the skull is ever seen in the transitory condition through which it passes, even in the earliest condition

<sup>1</sup> Virchow: Goethe als Naturforscher, 1861, S. 103.

of the embryo. The study of the embryonic or adult skull in man will not enable us, therefore, to determine, even approximately, the number of the primitive vertebræ through the fusion of which it has been developed. The researches of Gegenbaur<sup>1</sup> go to show, however, that the skull of the shark retains to some extent the primordial type of segmentation, in the fact of there being eight or nine branchial arches, and that the nerves emanating from the brain, excepting the olfactory and optic, bear to the latter the same relation that the spinal nerves bear to the spinal cord. If the latter be the case, and the branchial arches be regarded as homologous<sup>with</sup> with so many ribs, then the primitive cranium, in the shark, at least, must have been developed through the coalescence of so many vertebræ. Returning from this brief digression upon the nature of the primordial cranium in man to the thread of development, let us consider what becomes of these branchial arches. The visceral or branchial arches, resembling those of fishes, the intervening spaces between them being perforated by gill-like openings or slits, as in the latter animals, are four in number in man, and symmetrically disposed (Figs. 552, 575, 576), and are known from

FIG. 576.

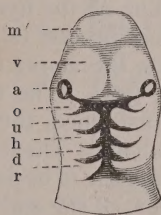
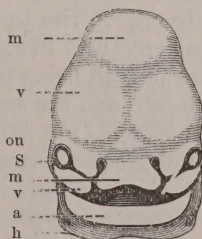


FIG. 577.



Visceral arches in man.

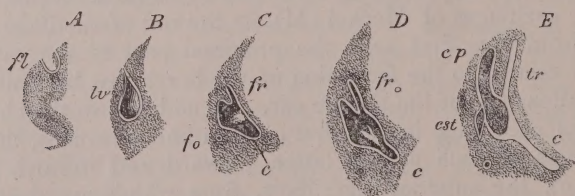
before backward as the first or mandibular (u), the second or hyoid (h), the third or thyro-hyoid (d), the fourth or subhyoid (r). Through the fusion at the middle line of the distal ends of the first visceral arches (Fig. 576, u), the rudimentary lower jaw (Fig. 577, a) is developed, the permanent jaw being developed by ossification (*mi*, Fig. 575) around the cartilages of Meckel (M), or the rod of cartilage that early appears within this first arch, the proximal part of the cartilages of Meckel not related to the formation of the lower jaw becoming eventually the malleus (m) of the middle ear. In addition to the changes just described as occurring in the first or mandibular arches, there grows from the root of each of the latter, forward and inward, a process (Fig. 576, o), the superior maxillary, from which are developed the superior maxillary and malar bones, and a pair of cartilaginous rods which ultimately become the pterygoid (o) plate of the sphenoid, and the palate bones, which lie parallel with the trabeculæ cranii. The latter are two elongated bands of cartilage at the base of the cranium, connected with the primitive auditory capsule, which diverging to enclose the pituitary body unite beneath the anterior end of the primordial cranium, to form the septum of the nose.

<sup>1</sup> Das Kopfskelet der Selachier, 1872.



The basis of the cranium consists, therefore, at an early period of development, of a cartilaginous rod developed around the notochord, and continuous where the latter ends, with the trabeculae cranii, the basi-occipital, basi-sphenoid, and presphenoid bones being developed in it by three centres of ossification, respectively; the vault of the skull, with the exception of the squamo-occipital—that is, the frontal, parietal, and squamous portion of the temporal bones—being developed directly out of membrane, instead of out of cartilage. During the development of the superior maxillary process from the first or mandibular arch, as just described, there grows downward, between the primitive olfactory grooves, later, the nostrils, the naso-frontal process (Fig. 576, m) or the termination of that part of the investment of the head situated beneath the fore-brain (v). In this way a large cavity is formed, bounded by the naso-frontal process above, the superior maxillary process at the sides, and the primitive lower jaw below, which later, through the inward growth and coalescence of the palatine plates, is subdivided into a mouth below and a nasal cavity above, the latter being further subdivided into two by the growth of the septum nasi—the tongue growing from the inner surface of the centre of the first gill arch. The second visceral arches, or hyoid arches (Fig. 576, h), growing downward, and fusing on the middle line, give rise to the lesser cornua of the hyoid bone, the stylo-hyoid ligament (Fig. 575, *stl*), and styloid process (*st*), the proximal portion of the arch being transformed into the stapes (*s*) and incus (*i*) of the middle ear, and the stapedius muscle (*sta*). The third visceral arches, the thyro-hyoid (Fig. 576, d), are transformed, through fusion, into the body and greater cornua of the hyoid bone. The fourth visceral arches, or the subhyoid (Fig. 576, r), do not appear to be developed into any particular organ, being situated in that part of the embryo which in the adult becomes the neck, and which is absent in the foetus. It has just been mentioned that the branchial arches in man resemble those of fish, in that the intervening spaces are perforated by slit-like openings or clefts, through which the water passes by which the vascular gills attached to the arches are bathed and the blood aërated in the latter animals.

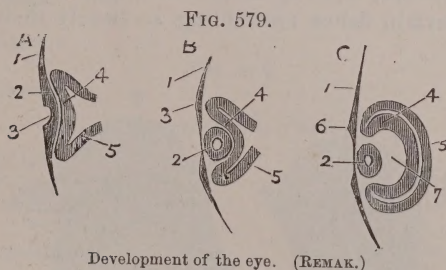
FIG. 578.



Development of the internal ear. (HÄCKEL.)

Apart, however, from the fact of the branchial arches in man never being fringed with gills, as in the fish, they ~~same~~ present another striking difference, in that these clefts all close up, save the first one, or that intervening between the mandibular and hyoid arches, which persists as the tympano-Eustachian tube—the latter being finally, in the adult, cut off from the exterior by the growing across it of the tympanic membrane.

Thus, through the transformation of the proximal ends of the first and second visceral arches, and of the cleft between them, the ear bones, meatus, tympanic membrane, tympanum, and Eustachian tube are formed, the external ear being developed from the integument near the first and second arches; the rudimentary internal ear through the invagination of that part of the epiblast situated immediately above the upper or proximal end of the second arch, which, in time closing (Fig. 578, *A fl*, *B lv*), becomes a vesicle. The latter, the rudimentary vestibule, in giving off successively the three semicircular canals (Fig. 578, *C*, *D*, *E*, *c*, *cp*, *est*), and the cochlea (*c*), originally a straight tube, develops into the internal ear of the adult. It will be remembered, in speaking of the functions of the ear, it was mentioned that the transitory stages through which it passes in its development are permanently retained as the organ of hearing in the lower animals. Like the ear, the eye—at least the anterior part of it—appears first as an invagination of the epiblast (Fig. 579, *A*, 1), which in closing up (Fig. 579, *B*, 2) and separating from the same gives rise to the crystalline lens (2). On the other hand,



through the invagination of the optic cup or vesicle—that is, the peripheral portion of the optic nerve—by the indenting into it of the lens, the inner surface of the cup becomes the retina (4), the outer the tapetum nigrum of the choroid (5), the vitreous humor being developed through the insertion of the mesoblast from below between the lens and the retina. The remaining portions of the eye are also developed out of the mesoblast, through the latter growing around the ball of the eye as a fibrous capsule, which splitting into an anterior and a posterior layer, gives rise to the sclerotic and cornea, and choroid and iris, respectively. Though the brain and spinal cord are developed out of the epiblast, the cranial nerves, with the exception of the olfactory and optic, which are outgrowths of the anterior cerebral vesicle, as well as the spinal nerves and sympathetic, are developed out of the mesoblast.

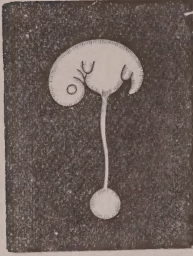
#### DEVELOPMENT OF ALIMENTARY CANAL AND ITS APPENDAGES.

The primitive alimentary canal, like the neural canal, extending as a straight tube from one end of the body to the other, is formed, as already mentioned, through the pinching off of the internal blastodermic membrane and the intestinal fibrous layers of the middle blastodermic membrane covering it, and by the bending inward and downward of the parietes of the body, the upper portion persisting in the adult as the



alimentary canal, the lower portion remaining only temporarily in the embryo as the umbilical vesicle (Fig. 580). At first the alimentary tube is closed at the ends, but as development proceeds

FIG. 580.

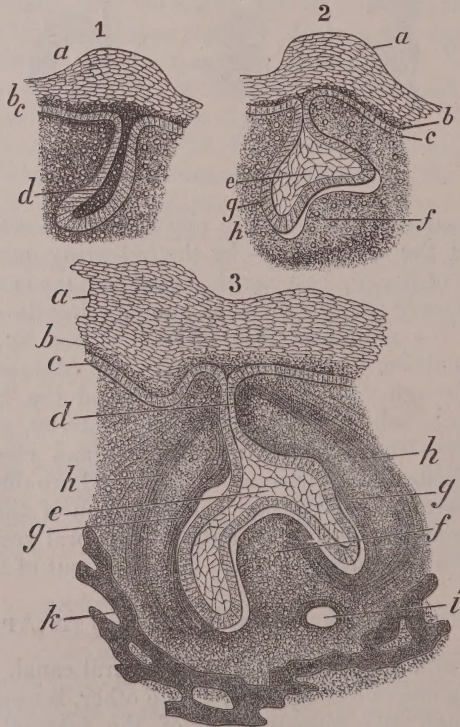


Human embryo, with umbilical vesicle; about the fifth week. (DALTON.)

the skin at both its extremities invaginating, deep furrows are formed, which, gradually growing toward the blind ends of the intestinal tube, finally break into the latter, and so give rise to the mouth and anus. Such being the manner in which these apertures are formed, it is evident that their lining membrane differs from that of the remaining portion of the alimentary canal in being developed out of epiblast instead of hypoblast. The mucous membrane of the mouth being then invaginated skin, the salivary glands, developed through the division and subdivision of its follicular glands, must be regarded as being essentially the same kind of glands as the sudoriparous and

sebaceous glands—that is, as epidermal in origin. Hence, also, the fact of the teeth of certain fishes resembling so closely their dermal spines,

FIG. 581.



Three stages in the development of a mammalian tooth germ. *a*. Oral epithelium heaped up over germ. *b*. Younger epithelial cells. *c*. Deep layer of cells, or stratum Malpighii. *d*. Inflection of epithelium for enamel germ. *e*. Stellate reticulum. *f*. Dentine germ. *g*. Inner portion of future tooth sac. *h*. Outer portion of future tooth sac. *i*. Vessels cut across. *k*. Bone of jaw. (From FREY.)

that at the border of the mouth it is difficult to say where the one <sup>set</sup>ends and the other begins. Indeed, teeth are simply calcified mucous membrane the invaginated oral epithelium (Fig. 581, 1, *d*), giving rise to the enamel, the submucous papilla (*f*) below, to the dentine, the pulp being made up of a matrix of connective tissue supporting bloodvessels and nerve fibres. The structure of the teeth having been already considered, it will not be necessary to dwell further upon them, merely calling attention to Table LXXXV., in which the order of development and appearance of the temporary and permanent teeth is synoptically given, and observing that while the permanent teeth are thirty-two, the temporary teeth are only twenty in number, the twelve permanent molar teeth not being preceded by corresponding temporary ones.

TABLE LXXXV.—ORDER OF DEVELOPMENT AND APPEARANCE OF TEETH.

| <i>Temporary.</i>          |                     |
|----------------------------|---------------------|
| (Intrauterine life.)       |                     |
| Kind.                      | Date of appearance. |
| Anterior molar . . . . .   | 7th week.           |
| Canine . . . . .           | 8th "               |
| Central incisors . . . . . | 9th "               |
| Lateral " . . . . .        | 9th "               |
| Posterior molars . . . . . | 10th "              |

| (Eruption after birth.)    |                |
|----------------------------|----------------|
| Central incisors . . . . . | 7th month.     |
| Lateral incisors . . . . . | 8th to 10th "  |
| Anterior molars . . . . .  | 12th to 18th " |
| Canines . . . . .          | 14th to 20th " |
| Posterior molars . . . . . | 18th to 36th " |

| <i>Permanent.</i>          |                                  |
|----------------------------|----------------------------------|
| Kind.                      | Date of appearance.              |
| First molar . . . . .      | 6½ to 7th <sup>year</sup> month. |
| Central incisors . . . . . | 7th to 8th "                     |
| Lateral incisors . . . . . | 8th to 9th "                     |
| First premolars . . . . .  | 9th to 10th "                    |
| Second premolars . . . . . | 10th to 11th "                   |
| Canines . . . . .          | 11th to 12th "                   |
| Second molars . . . . .    | 12½ to 14th "                    |
| Third " . . . . .          | 16th to 30th "                   |

The alimentary canal does not remain long in the human embryo a simple straight tube; its abdominal portion soon expands into the stomach, while through the elongation and coiling of the part immediately succeeding the latter, the small intestine is differentiated from the large one. It has been mentioned that the glandular structures of the alimentary canal are developed out of the hypoblast or its lining membrane. This is accomplished through the invagination of the latter into the wall of the alimentary canal, formed, it will be remembered, out of the intestinal fibrous layer of the mesoblast. The simple follicular glands so formed either remain as such, or, through elongation, become simple tubular glands, or, through segmentation, peptic or racemose glands. The liver and pancreas arise in a similar manner, the only essential

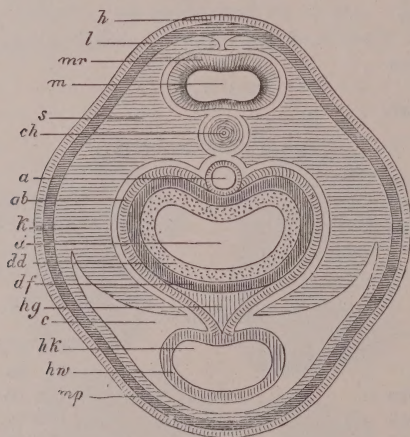


difference being that these glands enlarge enormously and recede to a considerable extent from the alimentary canal, with which they remain, however, through life in communication through their ducts. In the case of the liver, as already mentioned, the cells, like those of the remaining alimentary canal, are hypoblastic in origin, the fibrous capsule and vessels mesoblastic, the bile-ducts beginning as spaces between the cells.

#### DEVELOPMENT OF THE VASCULAR SYSTEM.

The heart, like the glands just mentioned, is also an appendage of the alimentary canal, but differs from the latter in being developed only out of the mesoblastic wall of the same. The heart is originally a mass of cells, but through liquefaction of the latter, or the primitive blood-corpuscles, is soon transformed into a muscular sac or tube, which remains for a short time connected by a mesentery (Fig. 582, *hg*) with the wall of the alimentary canal, of which it is, as

FIG. 582.



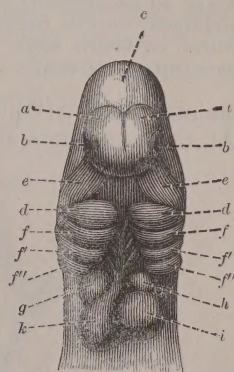
Diagrammatic transverse section through the head of an embryonic mammal. *h*. Epidermis-plate. *m*. Medullary tube (brain-bladder). *mr*. Wall of the latter. *l*. Dermis-plate. *s*. Rudimentary skull. *ch*. Notochord. *k*. Gill-arch. *mp*. Muscle-plate. *c*. Heart-cavity, anterior part of the body-cavity (*coeloma*). *d*. Intestinal tube. *dd*. Intestinal glandular layer. *df*. Intestinal muscle-plate. *hg*. Heart-mesentery. *hv*. Heart-wall. *hk*. Ventricle. *ab*. Aorta-arches. *a*. Transverse section through the aorta. (HECKEL.)

just said, an outgrowth. Coincidentally with the development of the heart, as just described, and in connection with it, there appears, apparently through fission of the inner and outer parts of the intestinal fibrous mesoblastic wall of the alimentary canal, the two primitive aortæ and the two primitive cardinal veins, respectively. The two primitive aortæ uniting then divide again, the two branches passing along the inner surface of the first visceral arches and curving around the anterior portion of the alimentary canal, unite anteriorly and pass as one tube into the heart aorta. At first there are but one pair of vascular arches encircling the alimentary canal; in time, however, five such are developed, three only coexisting at one period.

The primitive aorta further gives off lateral branches, of which two, passing to the umbilical vesicle, are known as the vitelline or omphalomesenteric arteries, while through the twisting of the heart into an S-like shape, the auricles become uppermost, the ventricles lowermost. Two veins, similarly named, return from the umbilical vesicle to the body of the foetus, and pass as a single trunk, the sinus venosus, into the heart. Such being the disposition of the heart and the primitive vessels, it follows that the nutritive material of the umbilical vesicle passes by the vitelline veins to the heart, and thence through the vascular arches to the primitive aorta and so to the body generally, the circulation being completed by the vitelline arteries. Neither the heart, aortic trunk, nor vascular arches remain, however, long in the condition in which they have just been described. The heart soon subdivides into a right and left heart through the growth of a longitudinal septum, and further into auricles and ventricles (Fig. 583) through the growth of transverse septa, the septum between the auricles remaining, however, incomplete until after birth, the opening so caused being known as the foramen ovale. Coincidentally with the development of the cavities of the heart through the growth of a longitudinal septum in the common arterial trunk, the latter subdivides into aorta and pulmonary artery, the aorta finally being disposed to the right, the pulmonary artery to the left. Finally through the transformation of the third, fourth, and fifth vascular aortic arches, the first and second having disappeared, the aorta and its first main branches and the pulmonary artery are developed, the change being brought about through the atrophy or hypertrophy of these arches respectively. Thus, for example (Figs. 584-587), through the persistence of the left fifth arch (5), the right disappearing, the internal half of it becomes the pulmonary artery (*p*), the external half the ductus arteriosus, the left fourth arch (4) becoming the permanent aorta and giving off the left subclavian artery (*s*), the right fourth arch developing into the innominate dividing into the right subclavian and right common carotid, the left common carotid being given off by the aorta, the third left arch (3) on both sides entering more into the formation of the internal carotid than of the external one, the outer connecting portions of the third and fourth arch disappearing.

With the establishing of the allantois, however, and the dwindling away of the umbilical vesicle, the allantoic or second circulation gradually replaces the vitelline or first one. The allantoic or umbilical veins, originally two in number, appear to be developed as branches of the vitelline veins, which, extending themselves through the allantois, finally pass into the villous processes of the chorion. Shortly after the appearance of the umbilical veins, the right one disappears, and with it

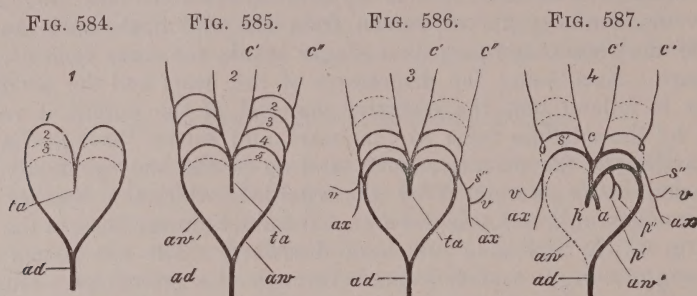
FIG. 583.



Heart and head of an embryonic dog, from the front. *a.* Fore-brain. *b.* Eyes. *c.* Mid-brain. *d.* Primitive lower jaw. *e.* Primitive upper jaw. *f.* Gill-arches. *g.* Right auricle. *h.* Left auricle. *i.* Left ventricle. *k.* Right ventricle. (BISCHOFF.)

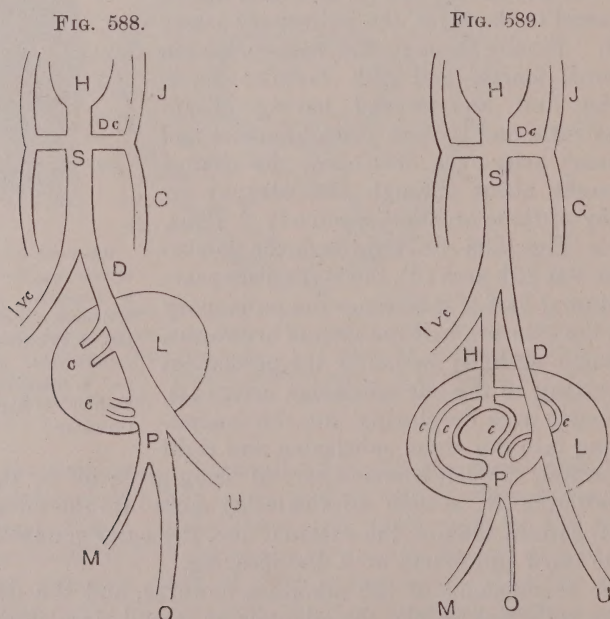


the right vitelline vein and that part of the left vitelline outside of the body of the embryo. The mesenteric portion of the latter, or left omphalo-mesenteric vein (Fig. 588, M), enlarges, however, while the re-



Metamorphosis of the five arterial arches in the human embryo. *ta*. Arterial stalk. 1, 2, 3, 4, 5, the arterial arches from the first to the fifth pair. *ad*. Main stem of the aorta. *av*. Roots of the aorta. In Fig. 584, three of the arterial arches are given; in Fig. 585, the whole five (those indicated by dots are not yet developed); in Fig. 586, the first two have again disappeared; in Fig. 587, the permanent arterial stems are represented. The dotted parts disappear. *s*. Subclavian artery. *v*. Vertebral artery. *ax*. Axillary artery. *c*. Carotid artery (*c'*, outer, *c''*, inner carotid). *p*. Pulmonary artery (lung-artery). (RATHKE.)

maining portion (O), that returning from the umbilical vesicle, atrophies. At the same time, the left umbilical vein (Fig. 588, U) becomes very



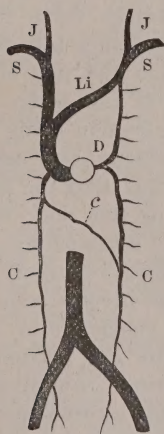
Diagrammatic view of portal and umbilical circulations.

Diagrammatic view of portal and umbilical circulations more advanced than in Fig. 588.

much enlarged, and as it is a branch of the omphalo-mesenteric vein, it will with the mesenteric branch of the same, pass as one trunk (P D) to the sinus venosus (S), and so reach the heart (H). The continuity, how-

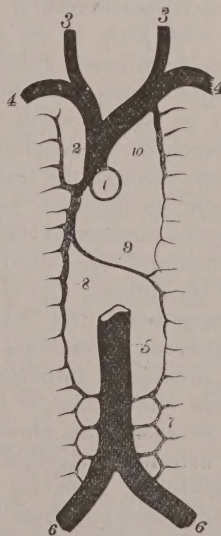
ever, of this trunk due to the union of the umbilical and omphalo-mesenteric vein, is interrupted by the development of the liver (L) as an investing mass around it, and by the appearance of the inferior vena cava. The latter may be regarded as the backward prolongation of the sinus venosus (S), and in dividing posteriorly into two branches gives rise to the two iliac veins. With the growth of the liver the common trunk (Fig. 589, P), which may now be called the portal vein, gives off capillaries (C C), which, ramifying through the liver, pass into the vena cava by a distinct vessel, the hepatic vein (Fig. 589, H). The amount of blood circulating through the hepatic capillaries (c c) at this period is, however, but small, since little blood comes from the intestines through the mesenteric vessel (M), while of the blood passing through the umbilical vein (U), the greater part flows directly through what may be now called the ductus venosus (D) into the inferior vena (Ivc), very little mixing with the blood of the portal vein (P). It will be remembered that the single aorta formed through the union of the vascular or branchial arches, passing from the heart along the inner surface of the visceral arches soon divides into the two primitive aortæ that run along toward the posterior end of the body on either side of the notochord. As development proceeds, the point of division of the aorta is carried much further back, its two branches becoming the iliac arteries.

FIG. 590.



Further development of the venous system. The cardinal veins (C) are diminished in size. The canal of Cuvier (D) on left side much atrophied. Primitive left innominate vein (Li), and primitive vena azygos minor vein (c) appearing. J, Jugular vein. S, Subclavian vein. (DALTON.)

FIG. 591.



Adult condition of venous system. 1. Right auricle of heart. 2. Vena cava superior. 3, 3. Jugular veins. 4, 4. Subclavian veins. 5. Vena cava inferior. 6, 6. Iliac veins. 7. Lumbar veins. 8. Vena azygos major. 9. Vena azygos minor. 10. Superior intercostal vein. (DALTON.)

From the internal part of the latter, that which becomes later the internal iliac arteries, two vessels are given off, which passing to the



allantois, give rise to the umbilical or hypogastric arteries. In the meantime the primitive cardinal veins (Fig. 589, C C) uniting with the jugular veins (J J), pass into the sinus venosus, and so to the heart, there being at this period then two superior venæ cavæ, a disposition which is retained during life in the elephant, manatee, rodents, monotremes, and birds. This condition, however, is only a transitory one, since a vessel (Li, Fig. 590) is given off from the point of union of the left jugular and subclavian veins, which uniting with the corresponding vessel of the right side forms the superior vena cava (2, Fig. 591), the left primitive superior vena cava almost entirely disappearing, being only represented in the adult by the coronary sinus and a fibrous band descending obliquely on the left auricle. Such being the disposition of the venous system with the establishment of the allantois (Figs. 589 and 590), or, as we shall see, presently, of the placenta, the heart in the meantime having become four chambered, the allantois or second circulation will be as follows: The blood returning from the head and upper extremities will pass to the right auricle of the heart by the superior vena cava, thence by the right ventricle and ductus arteriosus to the aorta, and so to the lower extremities, and to the allantois by the umbilical arteries. The latter being nourished by blood that has circulated through the head, etc., will be relatively, therefore, poorly nourished. On the other hand, the blood of the umbilical vein returning directly from the allantois or placenta laden with nutritive material and oxygen absorbed from the maternal blood will pass with little or no admixture from the portal blood into the right auricle, whence guided by the Eustachian valve it will pass through the foramen ovale into the left auricle, thence into the left ventricle, and so by the aorta to the head, hence the fact of the latter being so much better developed than the rest of the body. But little blood passes through the lungs in the foetus, aëration being effected by the placenta; on the other hand, a very large amount traverses the liver, which may be accounted for on the supposition that the liver acts as a decarbonizer of the blood, supplementing in this way the want of action of the lungs. At all events, with the establishing of the pulmonary respiration, the liver becomes smaller, relatively, while in animals, generally, the lungs and liver are in an inverse ratio as regards size and functional importance. With the replacing of the second or allantois circulation by the adult pulmonic and systemic circulations the foramen ovale closes, the ductus arteriosus, umbilical vein, and umbilical arteries <sup>are</sup> shrivelled up into cords, the internal portion of the latter remaining, however, pervious, and persisting in the adult as the superior vesicle arteries, while the part of the allantois remaining within the body becomes the urinary bladder and urachus.

#### DEVELOPMENT OF RESPIRATORY ORGANS.

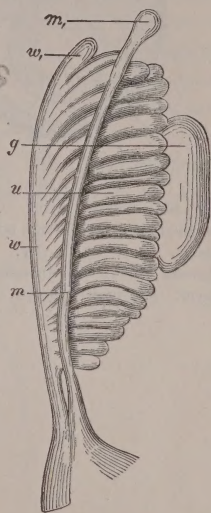
The respiratory organs may be regarded as appendages of the alimentary canal, since the trachea and œsophagus are originally one and the same tube. As development advances the trachea separates itself from the œsophagus, the upper portion becoming

the larynx, the lower subdividing into the two bronchi, the latter, by a process of fission and segmentation, giving rise to the bronchial tubes and pulmonary lobules.

### DEVELOPMENT OF THE GENITO-URINARY ORGANS.

The genito-urinary organs are so intimately associated in their development, that it will be found convenient to study them together. In describing the structure of the kidney, it was mentioned that however complex in structure the organ may appear to be, it consists essentially of a tube open at one end, from which are given off diverticula terminating in blind globular-like expansions. Such a primitive type of structure is presented through life in the kidneys of the myxinoid fishes, and as a transitory condition in man, in the early period of development. The common duct (Fig. 592, *w*), running from end to end of the body on either side of the notochord, which gives off the primitive urine tubes (Fig. 592, *u*), is known as the Wolffian duct (*w*), and is developed most probably out of the skin sensory layer (Fig. 593, *u*) by invagination and constriction, precisely as the spinal cord is developed, the duct, however, receding (Fig. 594, *u*) farther from the general surface of the body than the cord, and terminating in the cloaca or lower portion of the alimentary canal. Coincidentally with the development of the Wolffian duct and its diverticula, or the primitive kidneys, there appears in the mesoblast (Fig. 594) just at that part where the latter splits into the intestinal fibrous layer (*d*), and the skin fibrous layer (*h f*), the so-called indifferent gland, the cells of which differ in many respects from those of which the latter layers consist, and out of which the germinal epithelium (*g*, Fig. 595) giving rise to either ova or spermatozoa, as the case may be, appears to be developed. Such a condition of the urinary apparatus does not, however, remain long, there being developed out of the posterior portion of the Wolffian duct near where it passes into the cloaca a secondary duct, the primitive ureter, which gradually elongates and gives off diverticula, which become the renal tubules, and disposed with reference to the bloodvessels precisely as the diverticula of the Wolffian duct were. The urine excreted by the former, however, passes into the posterior part of the stalk of the allantois, or the urachus, which dilating, is retained in the body as the primitive bladder. The latter in time separates both from the cloaca and that part of the allantois which comes away as the umbilical cord and the foetal portion of the placenta.

FIG. 592.

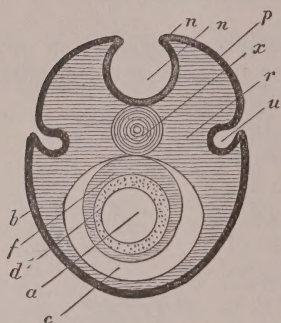


Primitive kidney of a human embryo: *u*. The urine-tubes of the primitive kidney. *w*. Wolffian duct. *w'*. Upper end of the latter (Morgagni's hydatid). *m*. Müllerian duct. *m'*. upper of the latter (Fallopian hydatid). *g*. Hermaphrodite gland, becoming either testicle or ovary. (KOBELT.)



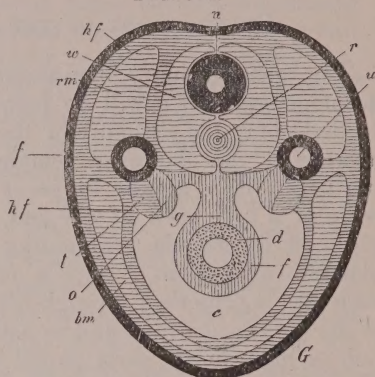
In this manner the permanent kidneys grow out of and replace the primitive ones developed out of the Wolffian duct. The latter, however,

FIG. 593.



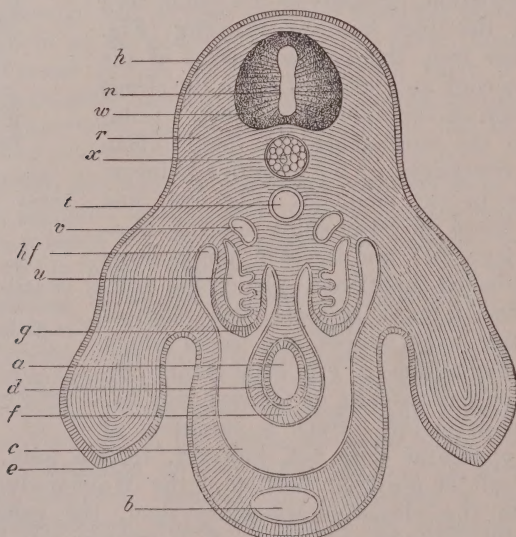
*h.* Skin sensory layer. *n.* Spinal tube. *u.* Beginning of Wolffian body. *x.* Notochord. *c.* Body cavity. *f.* Intestinal fibrous layer. *d.* Intestinal glandular layer. *a.* Intestinal tube.

FIG. 594.



*n.* Primitive spinal cord. *r.* Notochord. *hf* Skin fibrous layer. *w.* Vertebrae. *f.* Skin sensory layer. *rm.* Dorsal muscles. *bm.* Ventral muscles. *g.* Mesentery. *to.* Indifferent sexual gland. *d.* Intestinal fibrous layer. *f.* Intestinal glandular layer.

FIG. 595.



Transverse section through the pelvic region and the hind limbs of a chick, on the fourth day of incubation (about forty times the natural size). *h.* Skin sensory layer. *w.* Medullary tube. *n.* Spinal canal. *u.* Wolffian body or primitive kidneys. *x.* Chorda. *e.* Hind limbs. *b.* Allantois canal in the ventral wall. *t.* aorta. *v.* Cardinal veins. *a.* Intestine. *d.* Intestinal-glandular layer. *f.* Intestinal fibrous layer. *hf* Skin muscle layer. *g.* Germ-epithelium. *r.* Dorsal muscles. *c.* Body cavity (coeloma). (WALDEYER.)

do not disappear, but split (Fig. 596) into two distinct tubes, the outer still called the Wolffian duct (*w*), the inner the Müllerian duct (*m*).

The Wolffian duct, as just mentioned, for a time carries off the urine excreted by its tubules from the blood, but, as this office is transferred to the ureter and permanent kidneys, it gradually is transformed, if the individual becomes a male, into the epididymis and vas deferens, and will hereafter carry to the urethra the spermatozoa developed by the hitherto indifferent body (*ot*), now, therefore, a testicle; the Müllerian ducts, at their lower distal united portion, persisting as the sinus pocularis, the homologue of the vagina; the upper proximal portions as the so-called hydatid of Morgagni. On the other hand, if the individual becomes a female, the gland (*ot*) produces eggs, and is henceforth, therefore, an ovary. The Müllerian ducts fuse together from below upward and become the vagina, uterus, and Fallopian tubes; the Wolffian ducts persisting in an atrophied condition, in the human female, as the par-ovarium, or the white tortuous tubes in the broad ligament of the uterus; and in that of certain animals, the pig, as the ducts of Gaertner opening into the vagina. At an early period of intrauterine life the conjoined Wolffian and Müllerian ducts pass as the genital cord (Fig. 596, *gc*) into

FIG. 596.

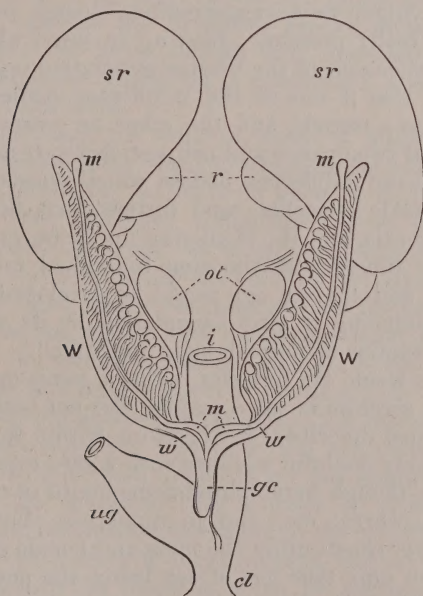


Diagram of the Wolffian bodies, Müllerian ducts, and adjacent parts previous to sexual distinction, as seen from before. *sr*. The suprarenal bodies. *r*. The kidneys. *ot*. Common blastema of ovaries or testicles. *W*. Wolffian bodies. *w*. Wolffian ducts. *m, m*. Müllerian ducts. *gc*. Genital cord, *ug*. Sinus urogenitalis. *i*. Intestine. *cl*. Cloaca. (QUAIN.)

the expanded stalk of the allantois, or urogenital sinus (*ug*); the latter, in time, emptying, together with the alimentary canal (*i*), into the cloaca (*cl*), or cavity common to both. As development advances, however, the rectum separates from the cloaca, and, if the individual becomes a



female, a further differentiation takes place, in that the lower united portion of the Müllerian ducts, or the vagina, terminates in an opening distinct from that of the urethra, or the passage-way from the bladder. The latter, in the case of the individual being a female, will pass beneath the clitoris, or female penis, the two adjacent folds of skin becoming the labia minora, the two latter external ones the labia majora, the ovaries lying within, in the body cavity. On the other hand, if the individual be a male, the urethra passes through the elongated penis; the under-skin of which is formed by the coalescence in the middle line of what, in the female, constitute the labia minora; the scrotum being formed through the fusion along the future raphe of the parts corresponding to the labia majora, into which the testicles descend by passing through the inguinal canal, the peritoneum consequently pushed in front of them becoming the tunica vaginalis testis. Such being the manner in which the external generative organs are developed in the two sexes, it will be readily understood why, in those male individuals, on the one hand, in which development is arrested at the stage at which the external generative organs in the two sexes are alike; and in the other, in those female ones in which the clitoris is much elongated, that such should be regarded by the vulgar as hermaphrodites, though in neither case is hermaphroditism really present. Bearing in mind what has just been said as to the development of the uterine generative organs, it is readily conceivable, also, that if one of the indifferent bodies of early <sup>ultra-</sup>uterine life, became a testicle, and the other an ovary, and both functionally active, or if two ovaries and two testicles were developed through the subdivision of the indifferent bodies, which consisted, probably, of both male and female elements; and further, that the Wolffian ducts became vasa deferentia, and the Müllerian ducts the vagina, uterus, and Fallopian tube or tubes; that the same individual might produce ova and spermatozoa, and that an egg might be developed in the uterus of the individual producing it after fecundation by its own spermatozoa, or by those of a similar or normal male individual. In such a hypothetical case there would be, however, either a penis or clitoris, but not both, and either a scrotum or labia majora, but not both. While a condition, like that just described, is, therefore, within the limits of possibility, it is extremely doubtful whether such a case ever actually existed in a human being, though hermaphroditism obtains in many of the lower animals, mollusca, worms, etc., and in numerous plants; the stamens and pistil of a flower constituting the male and female generative organs respectively. The only true test of sex being the power of producing ova or spermatozoa, it is obvious that however much the external or internal organs in any one individual may resemble those of the normal male or female as due to either hypertrophy or arrest of development, that such modified organs cannot be taken alone as an evidence of sex.

#### DEVELOPMENT OF EXTREMITIES.

The limbs first appear as bud-like protuberances from the sides of the body (Fig. 595, *e*), those giving rise to the upper extremities being developed first. While covered by the outer or skin sensory layer, the

limbs are developed more especially out of the deeper or skin fibrous layer, through its cells becoming first cartilage, with after-ossification of the same. As development advances, the primitive limb-bud recedes from the body, and expanding at its distal extremity, segments the divisions so arising, becoming, hereafter, the fingers and toes—the characteristic bones with the correlated muscles being gradually developed in the same.

### RÉSUMÉ OF DEVELOPMENT OF FŒTUS.

On the supposition that the ontogeny or development of the individual is the epitomized phylogeny or history of the race, we have some explanation of the fact that the various changes through which the embryo passes represent morphologically the permanent condition of lower forms of life. The principal changes undergone by the embryo during its development, which we have just endeavored to describe and account for, may be synoptically resumed about as follows :

At the twelfth day, the ovum, about 5 millimetres ( $\frac{1}{5}$ th of an inch) in length, consists of the zona pellucida beset with small villi, and enclosing a two-layered vesicle, the blastodermic vesicle.

At the fifteenth day, the embryo, about 2 millimetres (the  $\frac{1}{12}$ th of an inch) in length, exhibits the primitive groove, amnion, allantois, and umbilical vesicles ; the heart, though still one-chambered, is present, and the first or vitelline circulation is established, and the rudiments of the Wolffian duct indicated.

At the twentieth day, the embryo, about 3 millimetres ( $\frac{1}{8}$ th of an inch) in length, presents the visceral arches and perforated clefts.

At the twenty-first day, the embryo, about 4 millimetres ( $\frac{1}{6}$ th of an inch) in length, has developed rudimentary eyes, ears, mouth, three cerebral vesicles, and the heart has become four-chambered.

At the end of the first month the embryo has attained a size of 12 millimetres ( $\frac{1}{2}$  an inch), and is characterized by the presence of distinct rudimentary limbs, the whole ovum measuring about 17 millimetres.

At the end of the second month the embryo is about 25 millimetres (1 inch) in length, and weighs about 4 grammes ( $\frac{1}{8}$ th of an ounce), the whole ovum measuring about 7 centimetres (2.4 inches). By this time the vitelline vessels and right umbilical vein are obliterated, the future fingers and toes are indicated, the outer ear has appeared, nose and eyelids are present ; the umbilical cord is about 16 millimetres ( $\frac{3}{8}$ d of an inch) in length, and ossification has begun in the lower jaw, clavicle, ribs, vertebral bodies ; permanent kidneys present, but sex still indistinct.

At the third month the fœtus is about 10 centimetres (4 inches) in length, weighs about 20 grammes ( $\frac{3}{8}$ d of an ounce) ; a difference of sex is indicated by the external genitals, the umbilical cord is 7 centimetres (2.8 inches), and the placenta begins to be formed.

At the fourth month the fœtus is 17 centimetres (7 inches) long, weighs 120 grammes (4 ounces) ; umbilical cord is 19 centimetres (7 inches) long, and weighs 80 grammes (2.6 ounces).

At the fifth month the fœtus is about 20 centimetres (8 inches) in length, and weighs 284 grammes (9 ounces) ; the hair of the head and of the body, or lanugo, is quite distinct, and covered with the vernix



caseosa; the umbilical cord is about 31 centimetres (12 inches) long, and the placenta weighs 178 grammes (6 ounces).

At the sixth month the foetus is 28 centimetres (11 inches) long, and weighs 634 grammes (20 ounces), and meconium appears in the intestines.

At the seventh month the foetus is about 35 centimetres (14 inches) long, and weighs 1218 grammes ( $2\frac{1}{2}$  pounds); the eyes are open, one testicle has descended into the inguinal canal, and, if born at this period, is viable.

At the eighth month the foetus is 42 centimetres (16 inches) in length, and weighs between 1 and 2 kilos (2.2 to 4.4 pounds); one testicle has descended into the scrotum.

At the end of the ninth month, or at full term, the foetus is about 51 centimetres (20 inches) in length, and weighs  $3\frac{1}{4}$  kilos (7 pounds).

#### DEVELOPMENT OF THE PLACENTA.

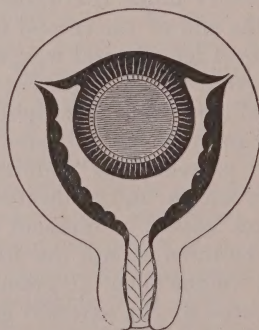
Up to the present moment nothing has been said as to the changes undergone by the mucous membrane of the uterus after the ovum has passed into the cavity of the same. These changes, which must now be at least briefly considered, appear to differ rather in degree than in kind from those exhibited by the mucous membrane during menstruation, the essential difference being that the mucous membrane during pregnancy is hypertrophied to a far greater extent, and more of it is finally cast off than during menstruation. As the fecundated egg passes through the Fallopian tube, the mucous membrane of the uterus becomes tumefied, vascular, and rugose, projecting as rounded eminences into the cavity of the uterus (Fig. 597), the uterine tubules at the same time elongating and expanding to such an extent that their open mouths become perceptible at the surface. The mucous membrane so modified is a thick, soft, velvety, vascular lining, quite different from that of the

FIG. 597.



Impregnated uterus, with projecting folds of decidua growing up around the egg. The narrow opening, where the edges of the folds approach each other, is seen over the most prominent portion of the egg. (DALTON.)

FIG. 598.

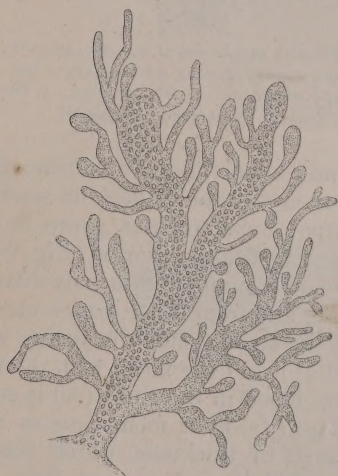


Impregnated uterus: showing connection between villusities of chorion and decidual membrane. (DALTON.)

unimpregnated condition; indeed, so much so that the decidua vera, as the membrane is now called, was supposed at one time to be of new formation.

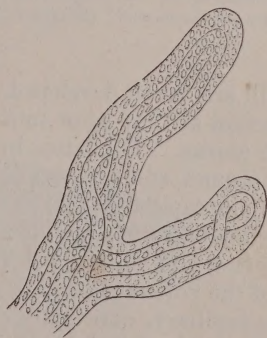
The decidua vera is, however, only the hypertrophied mucous membrane of the uterus, being continuous at the orifices of the Fallopian tubes with the mucous membrane lining the latter, and at the os internum with that lining the cervix. It should also be mentioned that at this period the cavity of the latter becomes so filled with a viscid-like mucus that the passage-way to the vagina is blocked up, the ovum within the cavity of the uterus being thereby protected from external influences. The impregnated egg having reached the uterine orifice of the Fallopian tube, passes through the latter into the cavity of the uterus and is caught, as it were, between a pair of the folds of the decidua vera and retained there by the growing downward and around of the latter, until the ovum is completely inclosed by the same. The reflected folds so developed are known as the decidua reflexa (Fig. 597), that portion of the decidua vera lying between the ovum and the wall of the uterus as the decidua serotina. It has already been mentioned that the chorion or vitelline membrane of the ovum at an early period of intrauterine life is covered with small villous-like processes, which in time become vascular through being penetrated by the bloodvessels of the allantois. The villi, when examined by the microscope (Fig. 599), present such a very characteristic appearance that their presence

FIG. 599.



Compound villosity of human chorion, ramified extremity. From a three months' foetus. Magnified thirty diameters. (DALTON.)

FIG. 600.



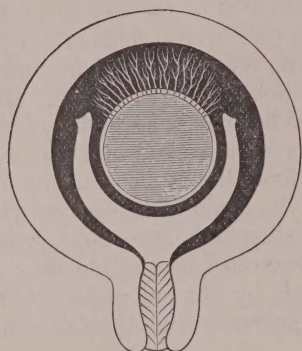
Extremity of villosity of chorion, more highly magnified; showing the arrangement of blood-vessels in its interior. (DALTON.)

may be accepted as positive proof of the existence of a foetus, as much so, indeed, as if the foetus itself had been found. The general appearance of a villus is like that of a sea-weed, originating in the chorion by a trunk, which divides and subdivides into filamentous branches, swollen here and there and terminating in rounded extremities, and consisting internally of a finely granular substance containing nuclei. At first the villous processes of the chorion are without vessels, but with the estab-



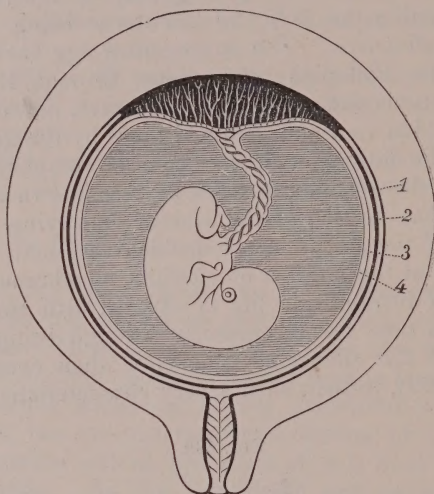
ishment of the allantois they become vascular through prolongation of the terminal allantoic vessels, which (Fig. 600) are disposed in loops. As development advances, however, the chorion loses its villi, except at that part of it in contact with the decidua serotina (Fig. 601), but here

FIG. 601.



Pregnant uterus: showing the formation of the placenta by the local development of the decidua and the chorion. (DALTON.)

FIG. 602.



Pregnant human uterus and its contents, about the end of the seventh month; showing the relations of the cord, placenta, and membrane. 1. Decidua vera. 2. Decidua reflexa. 3. Chorion. 4. Amnion. (DALTON.)

the villi are much developed, dividing and subdividing and insinuating themselves as they grow into the mucous membrane or decidua serotina of the uterus. The latter in the meantime hypertrophies, grows downward, around, and between the villous processes of the chorion (Fig. 603-605, *v*), its capillaries (*vc*) at the same time becoming enormously dilated, being finally transformed into sinuses into and from which pass a uterine artery (*ua*) and vein (*uv*). The wall of the sinus eventually fusing with that of the villous process of the chorion (*v*), and the latter with the wall of the capillary, eventually the maternal blood in the sinus (*vc*) is separated from the foetal blood in the villous (*fv*) by a membrane so thin as not to exceed the  $\frac{1}{4000}$ th of an inch in thickness, which readily permits of the osmosis of nutritive materials and oxygen from the mother's blood into that of the foetus, and of effete materials from the blood of the foetus into that of the mother, though at no time is there any connection between maternal and foetal vessels. The organ so formed, with nutritive and respiratory functions, is called the placenta, and evidently consists of two parts, foetal and maternal, the allantois and decidua serotina, which, however, become so intimately united that eventually they are inseparable, and are cast off as such during labor as the "after-birth." As development proceeds, the amnion becoming distended with the fluid given off by the foetus, consisting principally of water, some urea and alkaline salts, fuses about the fifth month of preg-

nancy with the decidua reflexa. The latter, in turn, fusing about the seventh month of pregnancy with the decidua vera, it so comes that at the end of pregnancy the foetus, suspended from the placenta by the umbilical cord, floats in the amniotic fluid, the enclosing sac of which, consisting of the three layers just mentioned, now fused together.

FIG. 603.

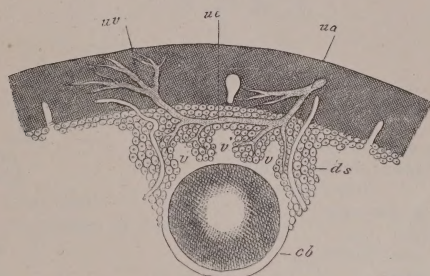


FIG. 604.

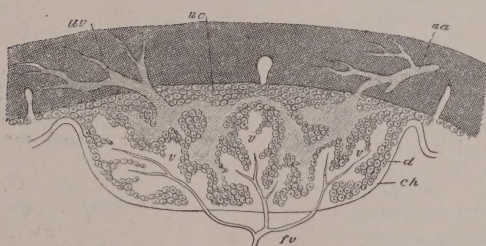
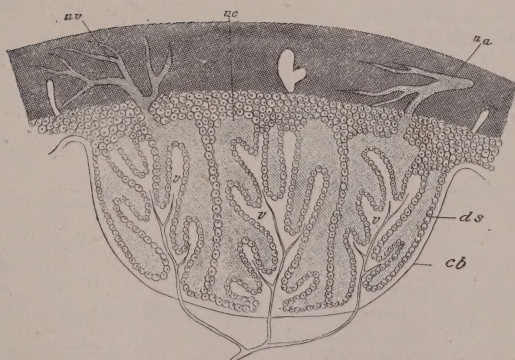


FIG. 605.



*ua.* Uterine artery. *uc.* Uterine capillary. *uv.* Uterine vein. *ds.* Decidua serotina. *ch.* Chorion.  
*v.* Villous processes of chorion. *fv.* Foetal vessels. (ERCOLANI.)

With the rupture of the latter and the escape of the water, etc., the child is born, and that life begins, which it has been the object of this work to endeavor to describe.





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